BOTTOM-UP FORCING OF GROWTH AND CONDITION CHANGES IN NORTHWEST ATLANTIC CAPELIN (*Mallotus villosus*) DURING THE 1990s: EVIDENCE FROM FEEDING INDICES

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Bottom-up forcing of growth and condition changes in Northwest Atlantic capelin (*Mallotus villosus*) during the 1990s: evidence from feeding indices

by

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Abstract

I investigated the persistence of changes in the biology of capelin (*Mallotus villosus*) of the northern Grand Banks ecosystem, in relation to the food web and other species. Comparisons of condition, size, and diet for capelin from the northern Grand Banks, northeastern Scotian Shelf and northern Gulf of St. Lawrence demonstrated that a lack of large zooplankton (euphausiids) in the Grand Banks capelin diet, following the cold period of the early 1990s, resulted in reduced growth (i.e. stunting) and condition. Examination of diet and stable isotope signatures of capelin and northern shrimp (*Pandalus borealis*) revealed no evidence of significant overlap in prey consumption. Thus, the increase in the abundance and distribution of pandalid shrimps during the 1990s likely did not contribute to the changes in capelin biology and feeding. All evidence pointed to bottom-up, not top-down, forcing of changes in capelin biology.

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INTRODUCTION AND OVERVIEW

Capelin (*Mallotus villosus*) is a short-lived, pelagic schooling species and an important forage fish for many fishes, marine mammals, and seabirds (Templeman, 1948; Dolgov, 2002; Friis-Rødel and Kanneworff, 2002). Capelin have a circumpolar distribution in the northern hemisphere, with major stocks/stock complexes in the north Pacific, Newfoundland and Labrador, the Barents Sea, Iceland, and west Greenland (Campbell and Winters, 1973; Vilhjálmsson, 1994).

Capelin, an important prey species in the Newfoundland food web, are a source of energy for fish, birds, and marine mammals (Templeman, 1948; Jangaard, 1974; Bowering and Lilly, 1992; Hammill and Stenson, 2000; Carscadden *et al.*, 2001). Historically, their greatest predator was the Atlantic cod (*Gadus morhua*) (Templeman, 1948; Campbell and Winters, 1973; Carscadden *et al.*, 2001), and capelin abundance and availability have been linked to cod growth (Jørgensen, 1992; Vilhjálmsson, 2002), condition, and gonad size (Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002).

Newfoundland Grand Banks capelin have been the subject of an inshore fishery, and an offshore fishery that was much smaller than those of Iceland and the Barents Sea (Templeman, 1948; Carscadden *et al.*, 2001). During the 1970s, a heavy offshore foreign fishery existed, peaking in 1976 with a catch of 246,000 t (Livingston and Tjelmeland, 2000). With the large reduction in capelin biomass during the late 1970s (Pinhorn and Halliday, 1990), the offshore fishery declined and eventually ended in 1992 (Carscadden *et al.*, 2001). Subsequently, capelin biomass increased greatly during the mid-1980s (Pinhorn and Halliday, 1990). During the late 1970s, the inshore fishery increased in

order to supply the Japanese market with roe-bearing females (Carscadden *et al.*, 2001), peaking at 80,000 t in the late 1980s (Livingston and Tjelmeland, 2000). Since the 1980s, capelin can be considered to have been only lightly exploited, as harvest rates were set at only 10% of the projected biomass and often did not exceed 5% (Narayanan *et al.*, 1995; Carscadden *et al.*, 2001).

The main body of research for capelin in the Northwest Atlantic exists for capelin off Newfoundland and Labrador. Templeman (1948) listed capelin as the second or third most valuable and abundant of all the fishes of inshore Newfoundland. Historically, capelin were found from Hudson Bay to the southern Gulf of St. Lawrence and were hypothesized to be of four different stocks: the northeast Newfoundland-Labrador stock, the Southeast Shoal stock, the St. Pierre Bank stock, and the Gulf of St. Lawrence stock (Campbell and Winters, 1973; Nakashima, 1992; Carscadden *et al.*, 2001). Pre-1990, capelin spent most of their lives on offshore banks, coming inshore to spawn on gravely beaches in the summer (late May to early July) (Templeman, 1948; Carscadden and Nakashima, 1997; Carscadden *et al.*, 2001), except for the Southeast Shoal stock which spawned offshore, believed to be the remnant of a beach spawning population that kept spawning in the same location after the beach became submerged about 12000 years ago with sea level rise accompanying retreat of the glaciers (Carscadden *et al.*, 1989). Prior to migrating inshore for spawning, capelin on the Grand Banks migrated south; their distribution was associated with temperature on larger spatial and temporal scales (Shackell *et al.*, 1994a). In the spring prespawning period, large schools tended to be present inshore on the Grand Banks, but not running on beaches (Templeman, 1948), with immature fish more northerly relative to mature fish (Shackell *et al.*, 1994a). Spawning

began first on the south coast and southern west coast and was latest in northern areas, including Labrador (Templeman, 1948).

Historically, capelin matured at 3-4 years of age, with an apparent size-at-age dependency for maturation (Winters, 1982). Females spawners ranged in size from 11-21 cm, while males were 13-21.5 cm, with the size of spawners declining throughout the spawning season, as larger fish typically spawned earlier than smaller fish (Templeman, 1948). Post-spawning survival was higher for females than for males, resulting in some females surviving to spawn in multiple years (Templeman, 1948; Shackell *et al.*, 1994b). Most larvae emerged in late June and early July (Templeman, 1948) and drifted southwards out of the bays of the eastern Newfoundland coast, such that adults exhibited a contranatant migration, migrating north to beaches to spawn (Nakashima, 1992).

Growth was latitude-dependent, with capelin in the Labrador area growing slower than those on the Grand Banks when young, although growth of Labrador capelin increased with age, thus allowing Labrador capelin to reach a slightly larger final size than Grand Banks capelin (Winters, 1982). In the inshore (Trinity Bay), overwintering capelin (February-March) had high fat content and heavy weight-at-length, compared to spring (April-May) prespawning capelin, whose fat content declined as their gonads developed and they approached spawning (Winters, 1970; Campbell and Winters, 1973).

Changes in the Northwest Atlantic ecosystem during the 1980s and 1990s

During the late 1980s and early 1990s the Northwest Atlantic experienced a period of below average temperatures (Drinkwater, 1996; Gilbert and Pettigrew, 1997;

Dutil *et al.*, 1999; Drinkwater, 2002; Drinkwater and Gilbert, 2004; Colbourne *et al.*, 2005). Coincident with low temperatures were changes in the distribution, abundance, growth, and biology of several species, which could not be fully explained by the overfishing of that era. The population of Atlantic cod collapsed to low levels (Lilly *et al.*, 2000; Drinkwater, 2002; Rose, 2004) and shifted its distribution more southerly, partially in response to changes in the distribution of capelin (deYoung and Rose, 1993; Rose *et al.*, 2000). American plaice (*Hippoglossoides platessoides*) populations declined dramatically and collapsed by the 1990s (Bowering *et al.*, 1997), as did several other demersal fish (Gomes *et al.*, 1995). Pelagic species showed divergent trends, with Arctic cod (*Boreogadus saida*) increasing in abundance (Lilly *et al.*, 1994; Gomes *et al.*, 1995), while the offshore abundance of capelin declined (Narayanan *et al.*, 1995; Carscadden and Nakashima, 1997). Changes in the ecosystem were reflected in the diet of northern gannets (*Sula bassanus*), which switched from a diet dominated by warm water species to one dominated by cold water species (mainly capelin) (Montevecchi and Myers, 1996). In addition, invertebrates were affected by these ecosystem changes. Lobster (*Homarus americanus*) numbers increased through the 1980s and peaked at high levels in the early 1990s (Parsons and Lear, 2001). Crab (*Chionoecetes opilio*) catches increased significantly during the 1990s, thus crab was inferred to have increased in abundance (Parsons and Lear, 2001; Dawe *et al.*, 2004). The abundance of pandalid shrimps also increased in the late 1980s and persisted through the 1990s, based on catch data (Lilly *et al.*, 2000; Parsons and Lear, 2001; DFO, 2006).

Changes in capelin biology on the northern Grand Banks

Capelin respond quickly to environmental change and have been thought to be an early indicator of ecosystem change (Rose, 2005). While offshore abundance of capelin declined unexpectedly between 1990 and 1991 (Miller, 1995; Miller, 1997), inshore abundance estimates in the region remained stable, with aerial surveys and trap estimates indicating no decline in the inshore abundance of capelin in Trinity Bay and Conception Bay prior to the spawning season (Nakashima, 1996; Nakashima and Borstad, 1997; Carscadden and Nakashima, 1997; Mowbray, 2001). Stable inshore abundance estimates matched well with cod feeding, which showed more capelin in the spring diet of cod in Trinity Bay, than in cod of the offshore Bonavista Corridor and Hawke Channel (Rose and O'Driscoll, 2002). At the same time as the decline in offshore abundance, the distribution of capelin shifted southward to centre on the northern Grand Banks (Carscadden and Nakashima, 1997; Anderson *et al.*, 2002), with capelin almost completely vanishing from Labrador (Carscadden *et al.*, 2001) and appearing on the Flemish Cap, the northeastern Scotian Shelf and the southern Gulf of St. Lawrence, well out of their normal range (Frank *et al.*, 1996; Carscadden and Nakashima, 1997). In addition, capelin modified their daily vertical migrations, spending more time closer to the seabed in both spring and autumn, resulting in decreased abundance in the upper layers of the water column (Mowbray, 2002).

Concurrent with the decline in offshore capelin abundance and the shifts in their distribution, capelin underwent several changes in their biology. The mean length of mature capelin decreased by several centimetres (Carscadden *et al.*, 1997; Carscadden *et*

al., 2002). This was attributed to a combination of capelin maturing at younger ages, with larger numbers of age 2 and 3 fish spawning, and decreasing sizes of older fish (Nakashima, 1994; Carscadden and Nakashima, 1997). The mean length of mature 2 year olds did not noticeably decrease, while mature 3-5 year olds were smaller (Nakashima, 1994). This has persisted into the 2000s, but no studies have addressed this trend (Carscadden *et al.*, 2001; Carscadden *et al.*, 2002). In conjunction with smaller sizes and the decreased temperature of the Grand Banks region, capelin spawning was several weeks later than historically (Therriault *et al.*, 1996; Carscadden and Nakashima, 1997; Carscadden *et al.*, 1997; Carscadden *et al.*, 2001; Nakashima and Wheeler, 2002), with the majority of spawners aged 2-4 (Nakashima, 1994). These late spawning times persisted into the 2000s (Carscadden *et al.*, 2002; Nakashima and Wheeler, 2002), despite an increase in ocean temperatures (Colbourne *et al.*, 2005), and are assumed to be the result of the continued small size of capelin (Carscadden *et al.*, 2002). These small capelin also were in poor condition (Carscadden and Frank, 2002). Females had below average condition (lower weight-at-length) in the mid-1980s through the 1990s, and during the late 1990s all males were in below average condition (Carscadden and Frank, 2002).

The apparent coincidence of changes in capelin distribution, abundance, growth and behaviour with the decline in Atlantic cod abundance and cooling ocean temperatures has led to several hypotheses on linkages among these factors and the changes in capelin. Lower sea temperatures were an obvious candidate as an underlying cause of capelin distribution shifts and lower growth (Carscadden and Nakashima, 1997; Carscadden *et al.*, 2002). However, as mean temperatures increased in the mid to late 1990s, capelin

remained southerly distributed, especially on the Scotian Shelf where temperatures remained below the long-term average (Carscadden *et al.*, 2001; Drinkwater and Gilbert, 2004), and the small mean size of mature capelin on the Grand Banks has persisted (Carscadden *et al.*, 2002). While temperature is important in determining the rate of growth in fish (Brett, 1979), studies on capelin indicate that a combination of temperature and zooplankton availability is more important (Gjøsæter and Loeng, 1987; Astthorsson and Gislason, 1998), since organisms cannot utilise or maintain the increased metabolic rates associated with increased temperature without increased energy intake (Brett, 1979). In Atlantic cod, Krohn *et al.* (1997) showed that 25% of the variability in growth of northern cod could be explained by temperature and capelin biomass, while those two variables explained 52% of the differences in condition. Reduced capelin growth and recruitment, in conjunction with low ocean temperatures and zooplankton production, have been seen in Iceland (Vilhjálmsson, 2002), but with the persistence of small sizes, despite increases in temperatures on the Grand Banks, it is unlikely that temperature alone is the causal factor for the continued small size of Newfoundland capelin.

The combination of the reduced size of capelin and the reduced abundance of Atlantic cod led to an intraspecific competition hypothesis, specifically that reduced predation by cod led to a dramatic increase in capelin abundance, and thus increased intraspecific competition for zooplankton prey, reduced capelin growth, and reduced zooplankton abundance (De Roos and Persson, 2002). This theory is not supported by the current evidence that the offshore abundance of capelin declined following the collapse of northern cod (Miller, 1995; Narayanan *et al.*, 1995; Miller, 1997; Carscadden and Nakashima, 1997). Nor has there been any evidence from acoustic surveys or stomach

analyses of capelin predators (e.g. Rose and O'Driscoll, 2002; Davoren *et al.*, 2006; F. K. Mowbray pers. comm.), that supported the existence of an increase in abundance of capelin in the Grand Banks region.

Shackell *et al.* (1994a) hypothesized that the southward migration of capelin in the spring was in search of a prey item that might maximize maturation during the important prespawning period. Based on preliminary stomach content analyses of spring capelin, Mowbray (2002) hypothesized that the changes in vertical distribution of capelin in the Grand Banks region might be explained by the reduced consumption of euphausiids. Continuous Plankton Recorder data indicated reduced euphausiid abundance in the region in the 1990s (Sameoto, 2004). Energetic or trophic bottlenecking, where the absence or low availability of an energetically important prey item leads to reduced predator growth (i.e. stunting), has been observed in freshwater fish (Persson, 1983; Heath and Roff, 1996; Sherwood *et al.*, 2002a) and Atlantic cod (Sherwood *et al.*, 2007). Energetic bottlenecking occurs when the energetic costs of activity (including feeding) are equal to the energy provided by feeding, thus leaving zero energy for growth (Sherwood *et al.*, 2002b). Thus, I hypothesized that Newfoundland capelin had become stunted due to the lack of an energetically important prey item in their spring diet (i.e. a dietary deficiency), a time when feeding intensity is increasing (Winters, 1970) and the development of energy-expensive gonads and secondary sexual characteristics is occurring (Winters, 1970; Karamushko and Christiansen, 2002).

The goals of this thesis were to expand our understanding of the persistence of changes in capelin biology on the northern Grand Banks based on a potential dietary deficiency, and to investigate a potential cause of energy deficient feeding through

comparison of a) spring diet, size, and condition of prespawning capelin from the Gulf of St. Lawrence (an area of stable abundance), the northeastern Scotian Shelf (an area of increased abundance) and the northern Grand Banks (an area of decreased abundance), and b) spring diets and stable isotope signatures of prespawning capelin and shrimp (*Pandalus borealis*), a species which has drastically increased in abundance on the northern Grand Banks, and may have competed with capelin for prey.

Capelin feeding and diet

Typically, the spring (April-May) is a period of intense feeding for capelin in the Newfoundland region (Winters, 1970). Feeding decreases in mid June, as the capelin approach the spawning beaches (Winters, 1970), increases again during the autumn (O'Driscoll *et al.*, 2001) and is reduced during the winter (Winters 1970; O'Driscoll *et al.*, 2001).

Capelin diets are similar across the species' range. In the Barents Sea, capelin growth at several life stages has been linked to the density or abundance of specific sizes of zooplankton (Gjøsæter *et al.*, 2002). The growth of young capelin is correlated with the abundance of small zooplankton including copepods, copepod nauplii and zooplankton less than 2000 μm, and the growth of older capelin is correlated with the abundance large zooplankton greater than 2000 μm including large copepods (*Calanus hyperboreus* and *Euchaeta* spp.), euphausiids, and amphipods (Gjøsæter *et al.*, 2002). In the Gulf of St. Lawrence, capelin historically shifted diet from small copepods to adult euphausiids, when capelin reached total lengths of 140 mm (Vesin *et al.*, 1981). Copepods, especially

Calanus finmarchicus, form an important part of capelin diet throughout the year, for fish of all sizes in the Barents Sea (Panasenko, 1978; Ajiad and Pushchaeva, 1992; Orlova *et al.*, 2002), near Iceland (Sigurdsson and Astthorsson, 1991), in the Bering Sea (Naumenko, 1984), and historically in the Gulf of St. Lawrence and on the Newfoundland and Labrador Shelf (Kovalyov and Kudrin, 1973; Chan and Carscadden, 1976; Vesin *et al.*, 1981; Gerasimova, 1994). Amphipods, and especially euphausiids, become more important than other prey items in larger capelin in all areas (Vesin *et al.*, 1981; Naumenko, 1984; Panasenko, 1984; Sigurdsson and Astthorsson, 1991; Ajiad and Pushchaeva, 1992; Huse and Toresen, 1996; Orlova *et al.*, 2002), especially during the prespawning season (Kovalyov and Kudrin, 1973; Panasenko, 1978; Gerasimova, 1994). More recent studies of capelin diet in the northern Grand Banks region showed copepods were the major prey across all seasons and capelin lengths, with reduced spring euphausiid feeding (O'Driscoll *et al.*, 2001), as compared with the 1970s and 1980s (Kovalyov and Kudrin, 1973; Gerasimova, 1994). Slightly higher spring euphausiid consumption by capelin has been recently seen in Trinity Bay (Pepin, 2006), and during the summer in northern Newfoundland (Davoren *et al.*, 2006).

A high capelin biomass reduces zooplankton abundance by grazing (Hassel *et al.*, 1991; Gjøsæter *et al.*, 2002) and capelin may show limited selectivity when feeding, as their diet is highly similar to the available zooplankton community (Astthorsson and Gislason, 1997). Although the feeding mode of capelin is unknown, a recent Newfoundland study by Pepin (2006) indicates that filter feeding is possible, although a combination of filter feeding and particulate feeding is seen in similar pelagic species.

Shrimp biology and feeding

During the period of below average temperatures in the late 1980s and early 1990s, when the biology of capelin in the Newfoundland region underwent several changes, the landings of the northern shrimp, *Pandalus borealis* (hereafter shrimp), increased (Lilly *et al.*, 2000; Parsons and Lear, 2001; DFO, 2006). Due to a lack of survey data, increased catch rates were assumed to be representative of increased abundance of shrimp, especially as the catch-per-unit-effort (CPUE) increased in the 1990s compared with the 1980s (Lilly *et al.*, 2000). Part of this upsurge in abundance of shrimp is thought to have been due to the decrease in Atlantic cod, a predator of pandalid shrimps (Lilly *et al.*, 2000; Worm and Myers, 2003). The importance of cod predation in the population dynamics of shrimp has also been seen in the Barents Sea, where there was a significant inverse relationship between shrimp abundance and frequency of occurrence in cod stomachs (Berenboim *et al.*, 2000). Part of the increase in shrimp abundance may also have been due to the decreased temperatures of the late 1980s and early 1990s providing more favourable conditions for pandalids (Anderson, 2000; Parsons and Colbourne, 2000). During the 1990s, the size of shrimp in the Newfoundland and Labrador region declined (Koeller *et al.*, 2007). The reduced size was hypothesized to have been partially the result of the changing environmental conditions (e.g. increasing temperatures) of the period (Koeller *et al.*, 2007), but even more of reductions in the intensity and delayed timing of phytoplankton blooms (Fuentes-Yaco *et al.*, 2007). In recent years, the size (Fuentes-Yaco *et al.*, 2007) and abundance (DFO, 2006) of shrimp have remained fairly stable.

Worldwide, few studies have been completed on the feeding of shrimp, with none in the Newfoundland region. Shrimp have been reported to feed extensively on zooplankton (including euphausiids and calanoid copepods) in the North Sea (Wienberg, 1981), the fjords of Norway (Hopkins *et al.*, 1993), the Barents Sea (Berenboim, 1981), England (Allen, 1966), and Alaska (Barr, 1970), especially during diel vertical migrations (Barr, 1970; Berenboim, 1981; Wienberg, 1981), in addition to feeding on the macrobenthos (Allen, 1966; Rice *et al.*, 1980; Berenboim, 1981; Wienberg, 1981). Berenboim (1981) showed that euphausiids and polychaetes were the main contributors to shrimp diet in the Barents Sea. Authors disagree on the relative importance of each portion of the diet, claiming either a mainly pelagic diet (Allen 1966; Barr, 1970; Hopkins *et al.*, 1993), a mainly benthic diet (Rice *et al.*, 1980) or recognizing the importance of each phase of feeding (Berenboim, 1981; Wienberg, 1981). In addition, there is no consensus in the literature on the importance of sediment or detrital feeding to shrimp. Some studies claim that detritus is not a nutritional contributor to the diet (Wienberg, 1981), while others report that 60% of stomach contents are sediment (Rice *et al.*, 1980). Hopkins *et al.* (1993) indicated that some shrimp lipids were possibly derived from detrital sources, but these lipids are not common in shrimp compared to other benthic feeding organisms. A recent mass balance modelling study in the Gulf of St. Lawrence used inverse modelling to calculate a 25% contribution of detritus to the diet of shrimp (Savenkoff *et al.*, 2006). Wienberg (1981) suggested that the ingestion of sand was an adaptation to replace the absence of a gastric mill in pandalid species.

There is no theory that accounts for all the observed changes in distribution and abundance of the fish and invertebrate species in the Northwest Atlantic. Notions that

temperature changes were the underlying cause of the poor growth in capelin and increase in shrimp do not explain why there has been no change in capelin condition or size with the warming ocean temperatures since 1996 (Drinkwater, 2002; Colbourne *et al.*, 2005). Alternatively, the impact of Atlantic cod predation release on shrimp (Lilly *et al.*, 2000; Worm and Myers, 2003) does not explain why cod's major prey, capelin, declined during the same period. Nevertheless, a more complex top-down cascade could have occurred (e.g. Worm and Myers, 2003; Frank *et al.*, 2005), in which the increase in shrimp, caused by release of predation pressure from cod, led to shrimp out-competing capelin for prey. This hypothesis depends on diet competition between shrimp and capelin, which is feasible, but has not been demonstrated.

Competition between shrimp and capelin might occur as a consequence of prey choice overlap, but no studies have been undertaken regarding competition between pandalid species and fish (Bergström, 2000). Allen (1966) investigated competition between *P. borealis* and *Pandalus montagui*, but determined that, as *P. borealis* was a more pelagic and active feeder than *P. montagui*, competition was unlikely to exist. Food competition between freshwater species can result in a smaller mean size of one of the competitors (Persson, 1983; Spencer *et al.* 1991) or reduction in the trophic level or diet breadth of the competitors (Persson and Hansson, 1999; Vander Zanden *et al.*, 1999).

Thesis Overview

In this thesis, I used measures of condition, size, and diet to elucidate the cause of the persistence of changes in the biology of capelin in the northern Grand Banks region,

in relation to changes in the food web, and the abundance of important species in the Northwest Atlantic ecosystem. In the first chapter of the thesis, a comparative approach, where size, condition, and diet of capelin were examined within regions in which capelin had declined (northern Grand Banks), increased (Scotian Shelf) and remained relatively stable (Gulf of St. Lawrence), was used to investigate the hypothesis that northern Grand Banks capelin have become stunted as a consequence of a dietary deficiency. Changes were compared to the long-term temperature and Continuous Plankton Recorder data for the region. In the second chapter of the thesis, the impact of the increased abundance of shrimp on capelin feeding, in the northern Grand Banks region, was investigated by comparison of diets and stable isotope measures (carbon and nitrogen) for both species, in relation to the hypothesis that prey consumption of capelin and shrimp overlapped significantly.

CO-AUTHORSHIP STATEMENT

I am the primary author of all research papers included in this thesis. I planned, designed and carried out the data collection in the field and lab, as well as requesting data from secondary sources. I was responsible for the data analysis and manuscript preparation. Dr. George A. Rose is the second author on all papers and provided advice and support during all stages of the thesis, including editing previous drafts.

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CHAPTER 1. STUNTED CAPELIN (*MALLOTUS VILLOSUS*): DIET AND ZOOPLANKTON EVIDENCE FOR BOTTOM-UP FORCING OF NORTHWEST ATLANTIC ECOSYSTEM CHANGE

1.1 Abstract

Capelin (*Mallotus villosus*) became stunted in northern Newfoundland waters during the cold period in the early 1990s. Stunting continued despite warmer conditions by 1996. I hypothesized that stunting resulted from a dietary deficiency that began in the early 1990s (food hypothesis). A comparative analysis of the condition, length-at-age and diet of capelin from the northeast Newfoundland Shelf and northern Grand Banks (NGB), northeastern Scotian Shelf (SS) and northern Gulf of St. Lawrence (NSL) in the spring of 2004, showed that maturing SS capelin grew faster and attained superior length and condition than NGB capelin (NSL capelin were intermediate but sample size was too low for statistical comparison). SS capelin fed heavily on euphausiids in contrast to NGB capelin that fed mostly on copepods. NSL capelin fed on a mixture of prey types, especially amphipods. A historical comparison of spring diets of Newfoundland capelin showed a steady decline in euphausiid consumption from the late 1980s onward, which was consistent with available Continuous Plankton Recorder data. The data suggest that bottom-up forcing of ecosystem change in the NW Atlantic has occurred, indexed by changing states of key zooplankters and capelin. The changes in available biomass of capelin likely influenced many marine predators, especially Atlantic cod (*Gadus morhua*).

1.2 Introduction

The Northwest Atlantic Ocean experienced below average temperatures during the late 1980s and early 1990s (Gilbert and Pettigrew, 1997; Dutil *et al.*, 1999; Drinkwater, 2002; Drinkwater and Gilbert, 2004). Coincidentally, several species exhibited changes in distribution, abundance, and growth that could not be fully attributed to the overfishing of that era, including groundfishes, such as Atlantic cod (*Gadus morhua*) (Rose *et al.*, 2000; Drinkwater, 2002) and American plaice (*Hippoglossoides platessoides*) (Bowering *et al.*, 1997), and pelagics, including Arctic cod (*Boreogadus saida*) (Lilly *et al.*, 1994; Gomes *et al.*, 1995) and capelin (*Mallotus villosus*), the dominant pelagic forage fish in the ecosystem (Frank *et al.*, 1996; Carscadden and Nakashima, 1997). Invertebrates were also affected, and over the same period there were large increases in the abundance and distribution of snow crab (*Chionocetes opilio*) (Dawe *et al.*, 2004) and pandalid shrimps (Lilly *et al.*, 2000; DFO, 2006).

Capelin respond quickly to environmental perturbation and have been thought to be an early indicator of ecosystem change (Rose, 2005). During the recent period of below average temperatures and changes in distribution and abundance, capelin distribution shifted southward, well beyond their typical range, to the Flemish Cap, Scotian Shelf, and southern Gulf of St. Lawrence (Frank *et al.*, 1996; Carscadden and Nakashima, 1997). Capelin around Newfoundland appeared to have reduced growth (i.e. were stunted), with the mean size of mature fish decreasing by several centimetres (Carscadden *et al.*, 2002). In addition, annual spawning timing was delayed (Carscadden

et al., 1997), body condition decreased (Carscadden and Frank, 2002), and daily vertical migrations became less apparent (Mowbray, 2002).

The changes in capelin distribution, abundance, growth, and behaviour that coincided with the decline in Atlantic cod and cooling ocean conditions, have led to several hypotheses on linkages among these factors. Lower sea temperatures were an obvious candidate as an underlying cause of capelin distribution shifts and slower growth (Carscadden and Nakashima, 1997; Carscadden *et al.*, 2002). However, as mean temperatures increased in the mid to late 1990s, capelin remained southerly distributed, especially on the Scotian Shelf where temperatures remained below average (Carscadden *et al.*, 2001; Drinkwater and Gilbert, 2004), and the small mean size of mature capelin in the Grand Banks waters persisted (Carscadden *et al.*, 2002). The reduced size of capelin led to an intraspecific competition hypothesis, specifically that reduced predation by cod had led to an increase in capelin abundance and reduced growth (De Roos and Persson, 2002). However, there is little evidence, from acoustic surveys or stomach analyses of capelin predators (e.g. Rose and O'Driscoll, 2002; Davoren *et al.*, 2006; F. K. Mowbray, pers. comm.), that supports the existence of increased capelin abundance in the Grand Banks region. Given these observations, I questioned if temperature or intraspecific competition were likely to be primary causal factors of the reduced mean size of capelin in Newfoundland waters. I hypothesized that stunting, in these capelin, resulted from the absence of an energetically important prey item, a dietary deficiency (the food hypothesis), which implicated ecosystem change at lower trophic levels. Energetic bottlenecking, where the absence or low availability of an energetically important prey item leads to reduced predator growth (i.e. stunting) due to increased foraging costs, has

been shown to reduce the maximum size of individuals in both freshwater fishes such as perch (*Perca flavescens*) (Sherwood *et al.*, 2002a) and in Atlantic cod (Sherwood *et al.*, 2007).

In this paper, the food hypothesis is tested. A comparative approach was used, whereby size, condition, and the diet of capelin were examined from regions where capelin had declined (northern Grand Banks region, hereafter NGB), increased (Scotian Shelf, hereafter SS), or remained relatively stable (northern Gulf of St. Lawrence, hereafter NSL). I used Continuous Plankton Recorder (CPR) data to examine changes in the plankton community with respect to the diets of capelin.

1.3 Materials and Methods

Capelin were collected from the NGB, the SS, and the NSL in the spring of 2004 (Figure 1.1). The widest possible range of sizes with a maximum of 100 fish per 1 cm size group were sampled (Table 1.1). Capelin sampling protocols for this study conformed to the methods of the Fisheries and Oceans Canada (DFO) annual capelin spring survey of the northern Grand Banks and Newfoundland Shelf (Mowbray, 2002). All capelin were measured for length (parallel to the lateral axis, from the tip of the snout to the upper lobe of the caudal tail) (± 1 mm), total body weight (± 0.1 g), stomach weight (± 0.01 g), and gonad weight (± 0.1 g); otoliths were removed for ageing. Fresh lengths were obtained for frozen specimens by multiplying thawed length by 1.03 (Winters, 1982). Sex and maturity were determined by visual inspection of the gonads. Maturing specimens were separated from immature ones by the presence of eggs/sperm, but were

not considered mature if the gonads were still small and sexual products were not free-flowing. Capelin stomachs were preserved in 5% formalin made with sodium borate-buffered seawater.

Stomach contents from the formalin-preserved stomachs were washed and examined with a dissecting microscope. Prey items were sorted into categories based on major taxonomic level (class or order) and wet weight was obtained for each category. Categories included copepods, euphausiids, mysids, hyperiid amphipods, gammarid amphipods, larvaceans, chaetognaths, molluscan larvae, pteropods, fish larvae, eggs, cirripedian larvae, brachyuran larvae, cladocerans, polychaetes, unidentified gelatinous material, and unidentified digested material. For hyperiid amphipods, fish larvae, euphausiids, and copepods, subsamples of up to 50 individuals per category were identified to species level (Bowman, 1973; Mauchline, 1984; Oake, 2001), and body length was measured. Total length, from the front of the eye to the tip of the tail along the lateral axis, was measured for all zooplankton except copepods, for which the lateral carapace length was measured. Wet weight of the subsample was recorded and compared to total category weight to estimate the total number of individuals of the prey category in the stomach. After analysis, all stomachs and prey items were preserved in 70% ethanol and saved for future identification.

CPR data were obtained from the Sir Alister Hardy Foundation for Ocean Science in Plymouth, England (SAHFOS) for euphausiids and the three most abundant *Calanus* copepod species (*C. hyperboreus, C. glacialis* and *C. finmarchicus*), in selected polygons on the NGB (data periods were 1960–1981, 1991–2005) and the SS (data periods were 1961–1976, 1991–2005) (Figure 1.1). The NSL was not included due to insufficient data.

CPR data provides an average number of individuals of each species per sample per month, based on samples of 3 m^3 of filtered seawater per 10 nautical miles (Richardson *et al.*, 2006). Monthly average number of individuals (n) was transformed to log (n+1). Yearly means of log abundance were then compared to the two overall means of log abundance, for all CPR data from the two time-periods, in each polygon.

Length frequency histograms were produced to check the overlap of size and maturity of capelin collected from the three areas. Fulton's K, a measure of weight-at-length, was used to assess condition in the maturing portion of the samples. Since gonad weight can account for a large portion of the total body weight in maturing capelin (Carscadden and Frank, 2002), Fulton's K here represents the somatic condition factor calculated as:

$$K = \{[\text{total body weight (g)} - \text{gonad weight (g)}]/L^3 \text{ (cm)}\} \times 10^3 \quad (1)$$

Analysis of covariance (ANCOVA) was used to test for significant differences of the condition-length regression between the NGB and SS. Mean length-at-age for maturing capelin in the NGB and SS was compared with Student's *t*-tests. NSL capelin were excluded from these analyses because of small sample size.

To assess stomach contents, four capelin groups (based on maturity and geographic region) were used: immature northern Grand Banks (NGB IM), maturing northern Grand Banks (NGB M), maturing Scotian Shelf (SS M), and maturing Gulf of St. Lawrence (NSL M). The small sample size of immature capelin from the NSL and the SS precluded their inclusion in these initial analyses. The five dominant prey categories, based on previous studies (Kovalyov and Kudrin, 1973; Panasenko, 1984; Gerasimova, 1994) and preliminary inspection, were: copepods, euphausiids, hyperiid amphipods, fish

larvae (*Ammodytes* sp.), and other prey. Frequency of occurrence of these five prey categories and of the dominant prey category in the stomach (by weight) were assessed for each group of capelin. Chi-square analyses of contingency tables tested for significant differences between the groups of capelin (Zar, 1999).

Subsequently, all immature and mature fish were pooled for each region and frequency of occurrence of the five dominant prey categories was investigated across capelin length (1 cm bins) for each region. Chi-square analyses of contingency tables tested for significant differences between the most frequent prey categories in each region and for those prey categories that occurred in >60% of the length bins (Zar, 1999). To test for size-selectivity in prey consumption, a regression of mean euphausiid length against capelin length was applied. A two-way analysis of variance (ANOVA) tested differences in the consumption of *Calanus* copepods by immature and mature capelin in the NGB region. For all analyses, the criterion for significance (α) was set at 0.05 and residuals were examined to evaluate the assumptions for p values. Due to the unequal variances across the two groups of capelin in the NGB, a more stringent α of 0.01 was set to reduce the chance of Type I error in this ANOVA.

Temperature data for 1980–2005 were obtained from the Meteorological and Environmental Data Service (MEDS) in Ottawa, Canada, for two regions: the Louisbourg Line on the northeastern Scotian Shelf (defined in Petrie *et al.*, 2005), and Station 27 on the northern Grand Banks (defined in Colbourne *et al.*, 2005). Temperature was vertically averaged in 60 m bins for all Station 27 temperature data at depths of 0-180 m and all data along the Louisbourg line at latitudes greater than 44°12′N and depths of 0-240 m. Using annual means for each region, vertically integrated temperature anomalies were

calculated for each year relative to the long term average (1980–2005), excluding data from 1987 and 1989 from the SS, due to a lack of data.

1.4 Results

Capelin from the SS achieved larger size than in the other regions: maturing SS females ranged in length up to 195 mm whereas fish >170 mm in length were rare in the other regions (Table 1.2, Figure 1.2). SS capelin length-at-age was greater in both sexes than in NGB capelin, with the exception of a small sample of age 3 males (Table 1.2). Sample size of age-sex groups limited comparisons with NSL capelin, which was dominated by males.

For maturing capelin, condition (Fulton's K) in SS capelin was significantly higher than in NGB capelin, in both males (ANCOVA, $F_{1,295}$=360.114, p<0.001) and females (ANCOVA, $F_{1,275}$=188.292, p<0.001) (Figure 1.3). Condition increased significantly with length for both males (ANCOVA, $F_{1,295}$=79.458, p<0.001) and females (ANCOVA, $F_{1,275}$=110.318, p<0.001) (Figure 1.3). Due to correlation between the variables, these p values were calculated by randomization (Jackson and Somers, 1991). Including stomach weight in the statistical model did not change the p value. NSL capelin, whose condition fell between the values for the other two regions, were not included in the analyses because of small sample sizes and restricted size range, but generally were intermediate between the high condition SS and low condition NGB capelin (Figure 1.3).

Stomach contents differed among the regions. For maturing capelin, the most frequent diet item on the SS was euphausiids, but in the NSL amphipods dominated, and on the NGB copepods were dominant in both maturing and immature capelin (Figure 1.4). Chi-square tests for independence showed a significant difference in the frequency of occurrence of all five major prey categories among the four capelin groups: copepods (χ^2=321.208, df=3, p<0.001), amphipods (χ^2=183.302, df=3, p<0.001), euphausiids (χ^2=567.211, df=3, p<0.001), fish larvae (*Ammodytes* species) (χ^2=76.678, df=3, p<0.001), and other prey (χ^2=63.648, df=3, p<0.001). Similar trends in diet occurred when stomachs were classified based on the dominant prey category by weight (Figure 1.5). Euphausiids dominated the stomach contents of maturing SS capelin but not in the other areas (χ^2=552.675, df=3, p<0.001); copepods were more dominant in the stomach contents of NGB fish than in the other areas (χ^2=289.555, df=3, p<0.001); amphipods dominated the stomach contents of maturing NSL capelin (χ^2=233.208, df=3, p<0.001) (Figure 1.5). Other prey were dominant in more stomachs of immature NGB capelin than in other areas (χ^2=19.590, df=3, p<0.001). Empty stomachs, accounted for in the percentage dominance method, showed a significant difference across the groups (χ^2=49.377, df=3, p<0.001), with the highest percentage occurring in the NGB, especially in immature capelin (Figure 1.5).

Frequency of occurrence of diet items by capelin length groups showed similar trends to the previous analyses (Figure 1.6). In NGB capelin, copepods were the most frequent prey item for all length classes, but amphipods were more frequently found in larger capelin (χ^2=77.665, df=10, p<0.001) (Figure 1.6). In SS capelin, euphausiids were the most frequent prey item for all capelin, independent of length (χ^2=12.169, df=9,

p=0.204), although the minimum expected cell frequency assumption was violated for the Chi-square test (Figure 1.6). For NSL capelin, amphipods were the most frequent stomach item across most lengths (except the 170 mm bin, n=2). Copepods also were fairly frequent items in NSL capelin stomachs across all lengths (Figure 1.6). Tests for significance in the NSL region failed to meet the minimum expected cell frequency assumption hence Chi-Square test results are not reported.

Historical studies have shown euphausiids to be a common diet item in NGB capelin (Table 1.3). In the springs of 1987–1990, euphausiids showed a 1.9-15.9% frequency of occurrence in immature capelin stomachs, compared with 0.0% in this study (Table 1.3). In maturing/mature capelin there was a steady decline since 1972 in the frequency of occurrence of euphausiids, which continued through the 1990s and early part of the 2000s (Table 1.3). For capelin with euphausiids in the stomach contents in this study, there was no significant difference in the mean length of euphausiids with capelin length, indicating a lack of size-selectivity for euphausiids by capelin ranging in length from 120-195 mm ($F_{1,148}$=1.547, df=1, p=0.215).

In NGB capelin, the dominant *Calanus* copepods were of three main species: the large Arctic species *C. hyperboreus* and *C. glacialis*, and the smaller arcto-boreal species, *C. finmarchicus*. The mean number of *Calanus* copepods increased with capelin maturity (two-way ANOVA, $F_{1,972}$=28.456, p<0.001), as did the number of larger *Calanus* species (two-way ANOVA, $F_{2,972}$=8.541, p<0.001) (Table 1.4). The mean number of individuals of the Arctic species (*C. hyperboreus* and *C. glacialis*) did not differ significantly, but the mean number of *C. finmarchicus* in stomach contents was significantly less than the mean number of the two Arctic species (*post hoc* Tukey tests; Table 1.4).

CPR data showed that during the 1960–1981 period euphausiid abundance was approximately equal on the SS and the NGB (Figure 1.7-A). The greatest regional difference in euphausiid abundance occurred from 1991–2005. In the early 1990s, both areas showed a decline in euphausiid abundance, but the SS showed a recovery in total euphausiid abundance during recent years, while the NGB has not (Figure 1.7-A). All stages of *C. finmarchicus* were more abundant on the NGB than on the SS, but no clear trends in abundance were evident during the last 40 years, except during the early 1990s when abundance declined in both areas, a trend clearly marked on the SS (Figure 1.7-B). Conversely, *C. hyperboreus* was less abundant during 1960–1981 and more abundant during 1991–2005; abundance did not differ between the NGB and the SS (Figure 1.7-C). *C. glacialis* showed a similar trend in abundance, but with more variability. In recent years (2000–2005), *C. hyperboreus* abundance appeared to be inversely related to *C. finmarchicus* abundance (Figure 1.7).

During 2001–2004, depth-averaged temperatures on the NGB at Station 27 were equal to or above the long term average, consistent with increased temperatures following the cold period of the early 1990s (Figure 1.8). SS temperatures, during the same period, were below the long-term average for the area (Figure 1.8).

1.5 Discussion

In the spring of 2004 maturing capelin on the SS had greater length-at-age than maturing capelin on the NGB and were in superior condition (higher adjusted Fulton's K). Newfoundland capelin can be considered to have been stunted, a phenomenon which

began in the early 1990s and is only beginning to abate in the mid-2000s (Carscadden *et al.*, 2002; G. A. Rose, unpublished data). Population length-at-age is a proxy for individual growth (Ricker, 1979), indicating higher growth rates of SS capelin compared to their NGB counterparts. Sea temperature differences between the two regions may account for part of these differences in growth (Brett, 1979), but the weight of the evidence does not support temperature as the main factor. The capelin studied were largely of the 2001 and 2002 year classes, and most would have reached maturity in 2004. Temperatures during this period were below average on the SS and above average on the NGB (Figure 1.8). In 2004, spring sea temperatures on the SS were 0–2°C (April-May) (Petrie *et al.*, 2005), only slightly warmer than on the NGB at Station 27 where temperatures were -1–2°C (April-May) (Colbourne *et al.*, 2005). Recent (post-2000) Station 27 temperatures have increased over those of the late 1980s to mid-1990s and NGB bottom temperatures since 1995 have increased to pre-1985 levels (Colbourne *et al.*, 2005; this paper). In contrast, recent SS temperatures have not increased relative to those of the mid-1980s to late 1990s (Petrie *et al.*, 2005; this paper), the period when capelin invaded the SS (Frank *et al.*, 1996). Hence, the marginally warmer conditions of the SS seem insufficient to account for the large difference in growth and condition of capelin from these two adjacent regions. In the Barents Sea, Gjøsæter and Loeng (1987) showed that increased growth in length is observed in capelin at increased temperatures, but that it only explains part of the variance in length. They concluded that observed increases in growth likely resulted from a combination of direct metabolic effects of increased temperatures and indirect effects through the increased availability of food. In general, warmer water will not result in increased growth if there is insufficient incoming energy

to meet increased metabolic costs and to provide sufficient energy for increased growth (Brett, 1979).

The data indicated that SS capelin fed primarily on euphausiids, a historically dominant food item for capelin in the Northwest Atlantic, but that NGB capelin fed primarily on copepods. These differences paralleled the observed differences in growth and condition, with euphausiid-feeding capelin (SS) achieving better growth and condition than those feeding on the smaller sized copepods and amphipods. That only 1.7% of maturing NGB capelin had consumed euphausiids contrasts sharply with both the historical importance of euphausiids in the prespawning period, in the vicinity of the NGB, and the present importance in the diets of the larger SS capelin. The present results are consistent with those from O'Driscoll *et al.* (2001), in which only 7.2% of all capelin from the NGB region had consumed euphausiids during the spring prespawning period, and of those, all were from the Trinity Bay area and not from the Grand Banks itself, where the present samples were taken and where the formerly large schools of juvenile and prespawning capelin aggregated (R. L. O'Driscoll, pers. comm.). Trinity Bay differs greatly in several respects from the Grand Banks and adjacent shelf areas, as it has maintained a relatively strong capelin presence throughout the 1990s (Carscadden and Nakashima, 1997; Nakashima and Borstad, 1997), and has been the centre of northern cod rebuilding (Rose, 2003). Relatively abundant euphausiid densities are also evident there based on acoustic and ROV surveys (G. A. Rose, unpublished data). Moreover, a recent study from the Trinity Bay region revealed that euphausiids constituted 22.9% of the capelin diet in July 2000 (Pepin, 2006).

Capelin diets are similar across the range of the species. In the Barents Sea, capelin growth at several life stages has been linked to the density or abundance of specific sizes of zooplankton (Gjøsæter *et al.*, 2002). The growth of younger capelin has been correlated with the abundance of small zooplankton including small copepods, copepod nauplii and zooplankton less than 2000 μm, while the growth of older capelin was correlated with the abundance of large zooplankton greater than 2000 μm including large copepods (*C. hyperboreus* and *Euchaeta* spp.), euphausiids, and amphipods (Gjøsæter *et al.*, 2002). In the Gulf of St. Lawrence, capelin diet shifts from small copepods to adult euphausiids, when capelin reach about 140 mm in total length (Vesin *et al.*, 1981). Copepods, especially *C. finmarchicus*, form an important part of capelin diet throughout the year for fish of all sizes in the Barents Sea (Panasenko, 1978; Ajiad and Pushchaeva, 1992), near Iceland (Sigurdsson and Astthorsson, 1991), and historically in the Gulf of St. Lawrence and on the Newfoundland and Labrador Shelf (Kovalyov and Kudrin, 1973; Vesin *et al.*, 1981; Gerasimova, 1994). Amphipods, and especially euphausiids, become increasingly important in the diets of larger capelin (Vesin *et al.*, 1981; Panasenko, 1984; Sigurdsson and Astthorson, 1991), especially during the prespawning season (Kovalyov and Kudrin, 1973; Panasenko, 1978; Gerasimova, 1994). It is anomalous that in the present study on the northern Grand Banks, capelin of all sizes consumed mainly copepods, with increased amphipod consumption only marginally evident in the largest fish, and no euphausiid consumption at all in any size group.

The absence of euphausiids in the stomachs of NGB capelin in the present study and the study of O'Driscoll *et al.* (2001) is consistent with the decreased abundance of euphausiids during the 1990s and 2000s on the NGB, as measured by the CPR data

(Figure 1.7). Taken together, these studies suggest that capelin feed on the most readily available large zooplankters. Although the CPR data were patchy, overall trends in euphausiid abundance in the Newfoundland area used in this study, and for the larger western Atlantic region (Sameoto, 2004) show lower abundance than in the 1970s, when Kovalyov and Kudrin (1973) observed that euphausiids formed 44.1% of capelin prey in the Grand Banks region. Euphausiid abundance on the Scotian Shelf, especially the northeastern region, declined in the early 1990s, but subsequently recovered (Sameoto, 2004; this study). Reduced euphausiid consumption during the 1990s has also been seen in murres (*Uria*) from the Newfoundland coast (Rowe *et al.*, 2000).

Historical evidence suggests that both immature and mature capelin (9-18 cm in total length) in Newfoundland fed heavily on euphausiids in the spring (Gerasimova, 1994). Energy density of euphausiids and copepods is similar (Griffiths, 1977; Mazur *et al.*, 2007), but euphausiids are larger and hence a more energetically favourable prey item, when available. Although the feeding style of capelin is unknown, rainbow smelt (*Osmerus mordax*), a member of the same family, are single-attack or particulate feeders (Mills *et al.*, 1995). With euphausiids apparently unavailable in the spring, NGB capelin have switched to copepod feeding, likely requiring multiple energy-expensive attacks, unlike SS capelin, which feed selectively on euphausiids with insignificant copepod uptake. Sherwood *et al.* (2002b) suggest that the energetic cost of multiple attacks on small prey is higher than that of searching for less abundant large prey. If true, the extra energy expended in foraging by large NGB capelin would have reduced the energy available for growth, effectively stunting the population. Furthermore, more NGB capelin had empty stomachs than SS capelin, indicating that the intensity of copepod feeding by

NGB capelin was not equivalent to the intensity of euphausiid feeding on the SS, regardless of the mode of capelin feeding.

On a broader spatial scale, the lipid profile of capelin in Canadian waters, historically, reflected a diet rich in copepods and euphausiids, based on the fatty acid signatures of prey items (Jangaard, 1974; Saether *et al.*, 1986; Falk-Petersen *et al.*, 1987), with capelin roe particularly high in lipids that are abundant in euphausiids (Jangaard, 1974; Henderson *et al.*, 1984). Capelin undergo rapid gonad development during the intensive prespawning feeding period from April/mid-May to mid-June (Winters, 1970). Euphausiid consumption may play an important role in gonad development (Gerasimova, 1994). Of note, maturation and gonad development of Newfoundland capelin has been delayed since the early 1990s (Carscadden *et al.*, 1997) and despite rising temperatures in Newfoundland waters, since 1995, these late spawning times have persisted, providing little support for the notion that temperature is the primary cause of these changes.

For maturing NGB capelin, condition appears to be unrelated to temperature (Carscadden and Frank, 2002). My data support this interpretation, as condition of NGB capelin did not increase from 1998 to 2004 as temperatures increased (Colbourne *et al.*, 2005). The superior condition of SS capelin, compared with NGB capelin, likely resulted from feeding on euphausiids in the spring; this also may explain why they were closer to spawning in late May to early June than were NGB capelin. Consuming lipids from euphausiids likely enhances gonadal development (Jangaard, 1974; Henderson *et al.*, 1984), requiring less lipid to be mobilized from muscle tissue stores, thus maintaining condition. That NGB capelin have matured later in the year and remained small and in poorer condition is consistent with the lack of euphausiids in their diet.

While euphausiids are important, especially in the prespawning season, *C. finmarchicus* forms an important part of the diet throughout the year and changes in abundance could impact condition in all seasons. General trends show a decline in the abundance of *C. finmarchicus* in the western Atlantic (Sameoto, 2004), although in the smaller spatial area investigated in this study there is no clear decline in abundance (Figure 1.7). Concurrent with this decline in *C. finmarchicus*, there was an increase in the large Arctic copepods, *C. hyperboreus* and *C. glacialis*, (Johns *et al.*, 2001), which show up in larger numbers in the diet of both immature and maturing capelin in Newfoundland (Table 1.4). Increased consumption of these copepods may compensate for the lack of *C. finmarchicus* and euphausiids in the diet of immature capelin, but not of maturing capelin. The relatively sudden appearance of Arctic zooplankton likely reflects distributional changes related to changing sea temperature.

The reason for the decline in euphausiids on the northern Grand Banks is less clear. No doubt the decline is related to physical or biotic conditions at lower trophic levels, and perhaps to climate change. The present data cannot resolve such questions, but a few comments may be in order. A link to sea temperature is problematic (with present data). If decreased temperature on the Newfoundland Shelf was responsible for the low euphausiid abundance, then as temperatures rose after 1995, a corresponding increase in euphausiid density and consumption by maturing capelin might be expected, but was not observed. Perhaps there is a longer time-lag (decadal) required to rebuild euphausiid stocks. In an attempt to link zooplankton and capelin production, Carscadden *et al.* (1997) suggested that cold years resulted in later zooplankton production, thus causing delayed feeding and maturation of capelin, but the peak spring bloom timing for euphausiids on

the Newfoundland Shelf has remained relatively constant throughout the 1990s up to 2003 (Maillet and Pepin, 2005), so if euphausiids were available they should have appeared in the capelin diet, as they did historically. It is also feasible that increases in Arctic cod (Lilly *et al.*, 1994; Gomes *et al.*, 1995) and pandalid shrimps (Lilly *et al.*, 2000; DFO, 2006), which both have a diet overlap with capelin (Bergström, 2000; Orlova *et al.*, 2002), negatively affected the capelin food supply through direct/indirect competition.

In conclusion, the study supports the food hypothesis. In brief, a dearth of large plankton (euphausiids) prevented NGB capelin from obtaining sufficient energy for growth and reproduction during and following the cold period in the early 1990s, thus reducing growth (i.e. stunting) and likely abundance. In contrast, SS capelin had access to sufficient energy for rapid gonad formation, thus achieving sizes (at-age) greater than historic means. There is little support for the temperature hypothesis as a main cause of these observed changes. In contrast, the intraspecific competition hypothesis appears to be a theoretical construct with no evidentiary support from this or other studies (e.g., Frank *et al.*, 1996; Rose and O'Driscoll, 2002). Finally, several hypotheses have been advanced that changes in the ecosystem of the Northwest Atlantic have resulted from so-called "top-down" influences of predation from harp seals (*Phoca groenlandica*) (Lilly and Murphy, 2004) or the release from predation by cod or other groundfish (Carscadden *et al.*, 2001; Frank *et al.*, 2005; Worm and Myers, 2003). The present work does not refute these notions, but does provide evidence of bottom-up forcing of the vital rates of the key pelagic prey species in the ecosystem, the capelin. The importance of capelin to consumers in the ecosystem is well know (Carscadden *et al.*, 2002; Rose and O'Driscoll,

2002; Vilhjálmsson, 2002), hence it is likely bottom-up forcing has propagated up the food chain influencing not only declines in several capelin eating species, but also their recovery (or lack of it).

Table 1.1 Capelin sample collection from the northern Grand Banks (NGB), Scotian Shelf (SS), and northern Gulf of St. Lawrence (NSL), during 2004. NGB capelin were collected during the annual DFO capelin acoustic survey of the northern Grand Banks, SS capelin were collected during the DFO spring shrimp survey of the northeastern Scotian Shelf, and NSL capelin were collected by fisheries observers from the bycatch of a commercial shrimp trawler.

Region	Date	Gear	Depth (m)	Duration (min)	Condition	n
NGB	Mid to late May	Campelen 1800 trawl, IGYPT midwater trawl	20-310	11-60	Fresh	499
SS	Early June	Shrimp trawl	239-329	30	Frozen	295
NSL	Mid June	Shrimp trawl	290	285	Frozen	88

Table 1.2 Mean length (mm) and standard error (mm) of maturing capelin from the northern Grand Banks (NGB) and Scotian Shelf (SS), during spring 2004.

		Males				Females			
Age	Region	n	Mean	SE	p[a]	n	Mean	SE	p[a]
2	NGB	64	152.84	1.271	<0.001	69	134.49	1.367	<0.001
	SS	149	161.15	0.875		80	150.38	0.397	
3	NGB	71	166.96	0.752	0.037	48	151.81	1.246	<0.001
	SS	11	162.18	3.074		10	168.80	2.682	
4	NGB	2	177.00	2.000	—	30	164.30	0.921	<0.001
	SS	0	—	—		35	180.37	0.933	
5	NGB	0	—	—	—	1	165.00	—	—
	SS	0	—	—		4	186.75	2.250	

[a]Based on Student's t-tests. Dash ("—") indicates that samples were too small to test statistically.

Table 1.3 Frequency of occurrence of euphausiids (%) in non-empty capelin stomachs, from spring studies of capelin in the northern Grand Banks region. This study shows a frequency of occurrence of 1.0%, if the samples are not split by maturity.

Collection date				
Year	Month(s)	Capelin maturity	Euphausiid frequency (%)	Reference
1972	March to June	Unknown	44.1	Kovalyov and Kudrin, 1973
1987	April to May	Immature	15.9	Gerasimova, 1994
		Mature	30.7	
1988	April to May	Immature	1.9	Gerasimova, 1994
		Mature	14.6	
1989	April to May	Immature	8.8	Gerasimova, 1994
		Mature	35.9	
1990	April to May	Immature	4.4	Gerasimova, 1994
		Mature	28.2	
1999	May to June	Unknown	7.2	O'Driscoll *et al.*, 2001
2004	May	Immature	0.0	Present study
		Maturing	1.7	

Table 1.4 Species composition of calanoid copepods in the stomachs of capelin collected from the northern Grand Banks region, during spring 2004. Values are reported as mean number and standard error, per capelin stomach.

	Calanus species					
	finmarchicus		*glacialis*		*hyperboreus*	
Capelin maturity	Mean	SE	Mean	SE	Mean	SE
Immature (n = 115)	0.57[a]	0.15	1.37	0.29	1.74	0.46
Maturing (n = 211)	1.67[a]	0.25	4.46	0.66	4.32	0.54

[a]Post *hoc* Tukey test shows a significant difference of $p<0.001$.

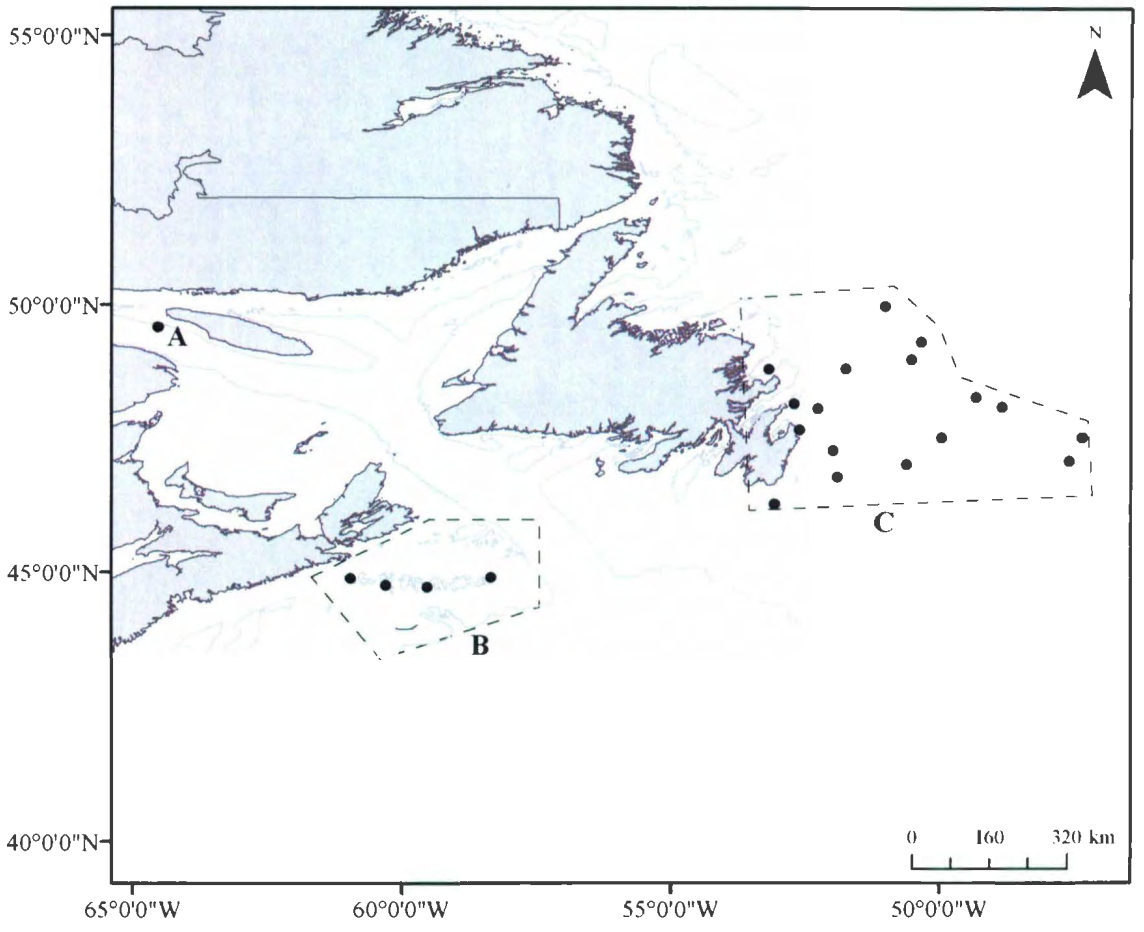

Figure 1.1 Sample sites in the northern Gulf of St. Lawrence (A), northeastern Scotian Shelf (B), and northern Grand Banks (C), during spring 2004. The dashed lines outline areas from which Continuous Plankton Recorder data were analyzed.

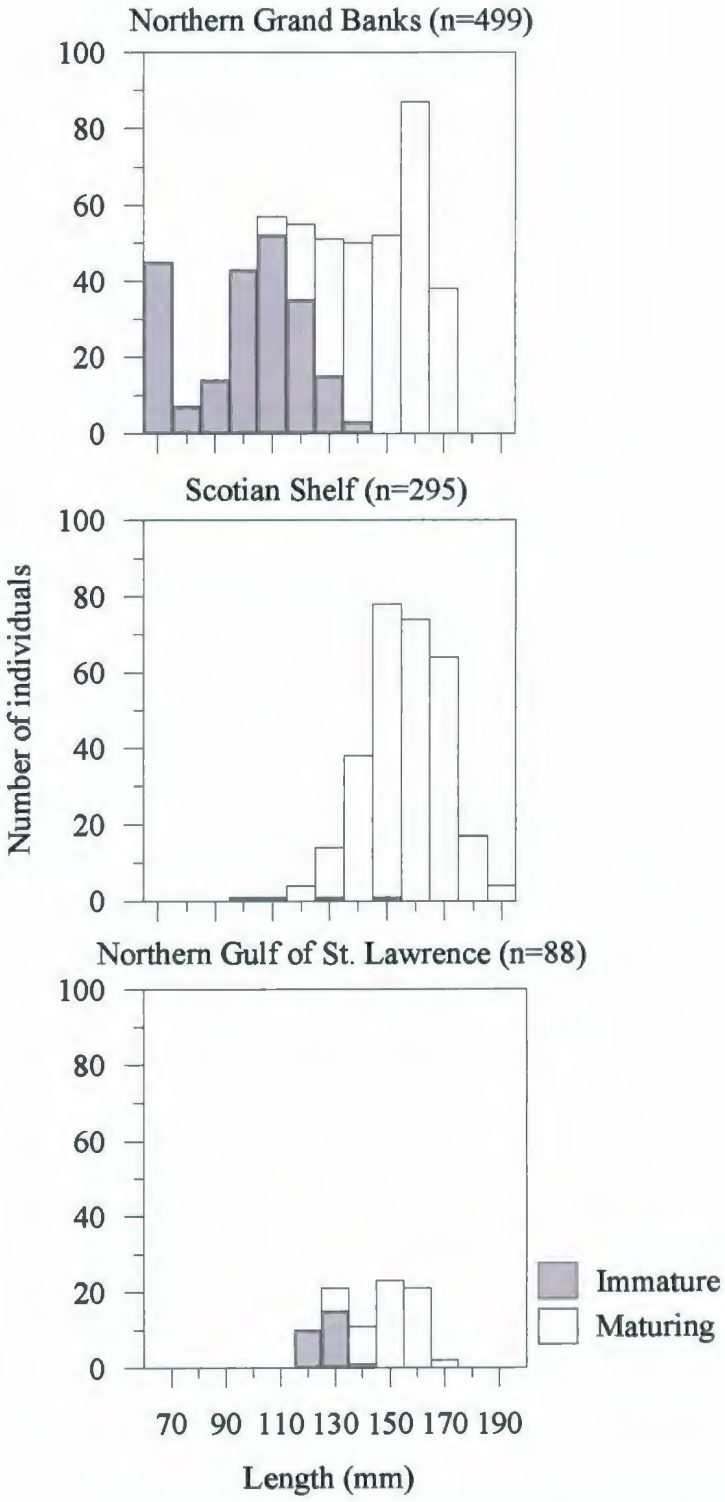

Figure 1.2 Length frequency of capelin from the northern Grand Banks, Scotian Shelf, and northern Gulf of St. Lawrence, collected during spring 2004.

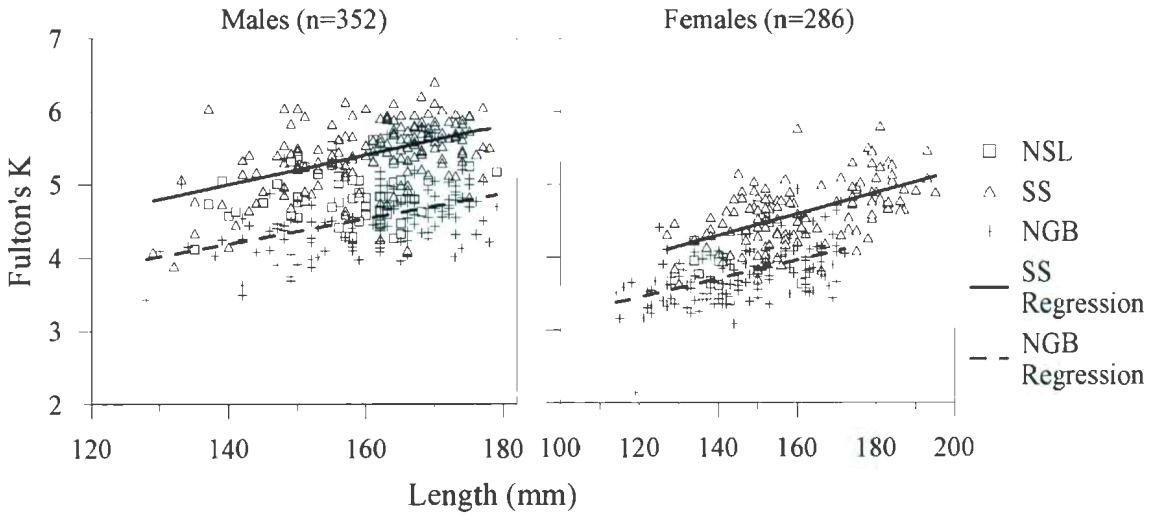

Figure 1.3 Condition (Fulton's K) of maturing males and females from the Scotian Shelf (SS, Males: n=161; Females: n=130), northern Grand Banks (NGB, Males: n=137; Females: n=148), and northern Gulf of St. Lawrence (NSL, Males: n=54; Females: n=8) in the spring of 2004. Regression lines were fitted for NGB males (Y = 0.017 * X + 1.782), SS males (Y = 0.020 * X + 2.182), NGB females (Y = 0.012 * X + 1.918), and SS females (Y = 0.015 * X + 2.231).

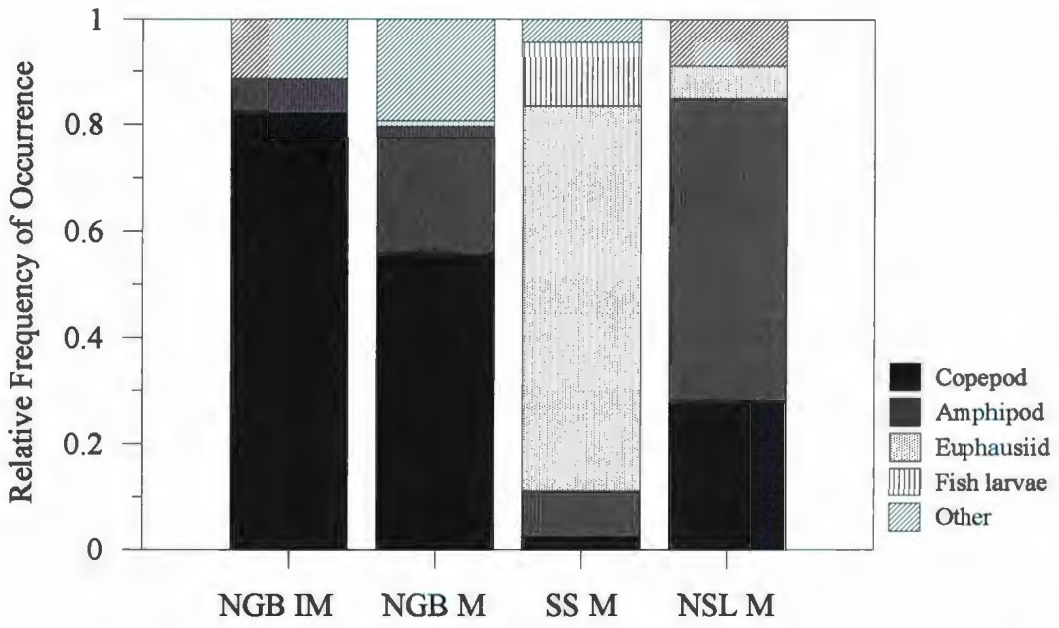

Figure 1.4 Relative frequency of occurrence of main prey categories for capelin from the northern Grand Banks (immature (NGB IM) and maturing (NGB M)), Scotian Shelf (SS M), and northern Gulf of St. Lawrence (NSL M), in the spring of 2004.

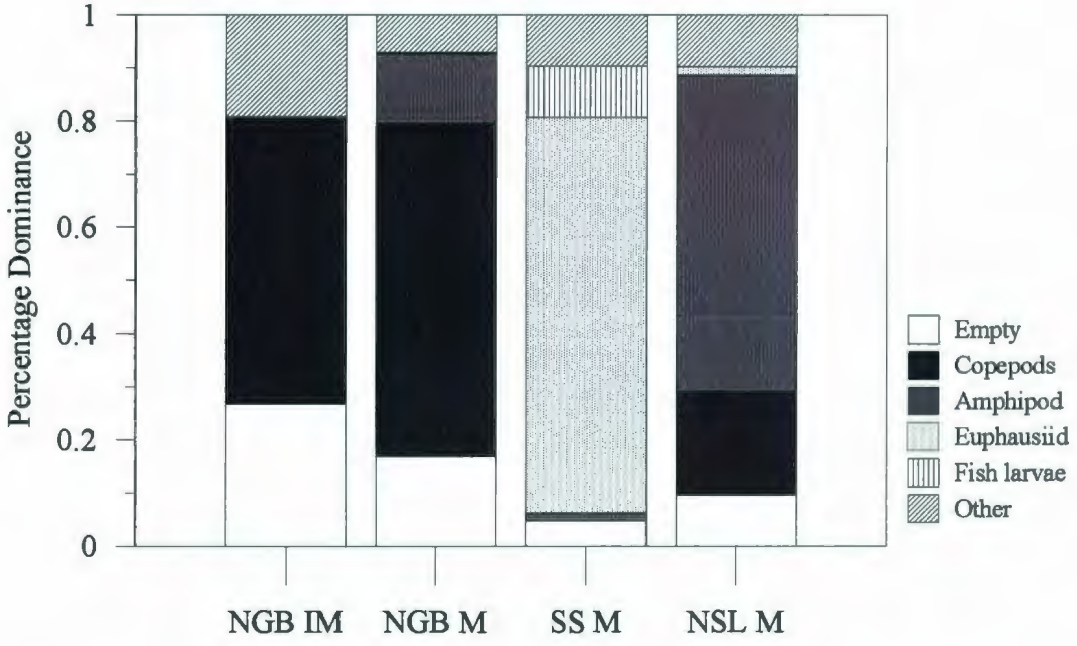

Figure 1.5 Percentage dominance (defined as the prey category constituting the highest weight in each stomach) of prey categories, for immature and maturing capelin from the northern Grand Banks (NGB IM and NGB M, respectively), and maturing capelin from the Scotian Shelf (SS M) and northern Gulf of St. Lawrence (NSL M), in the spring of 2004.

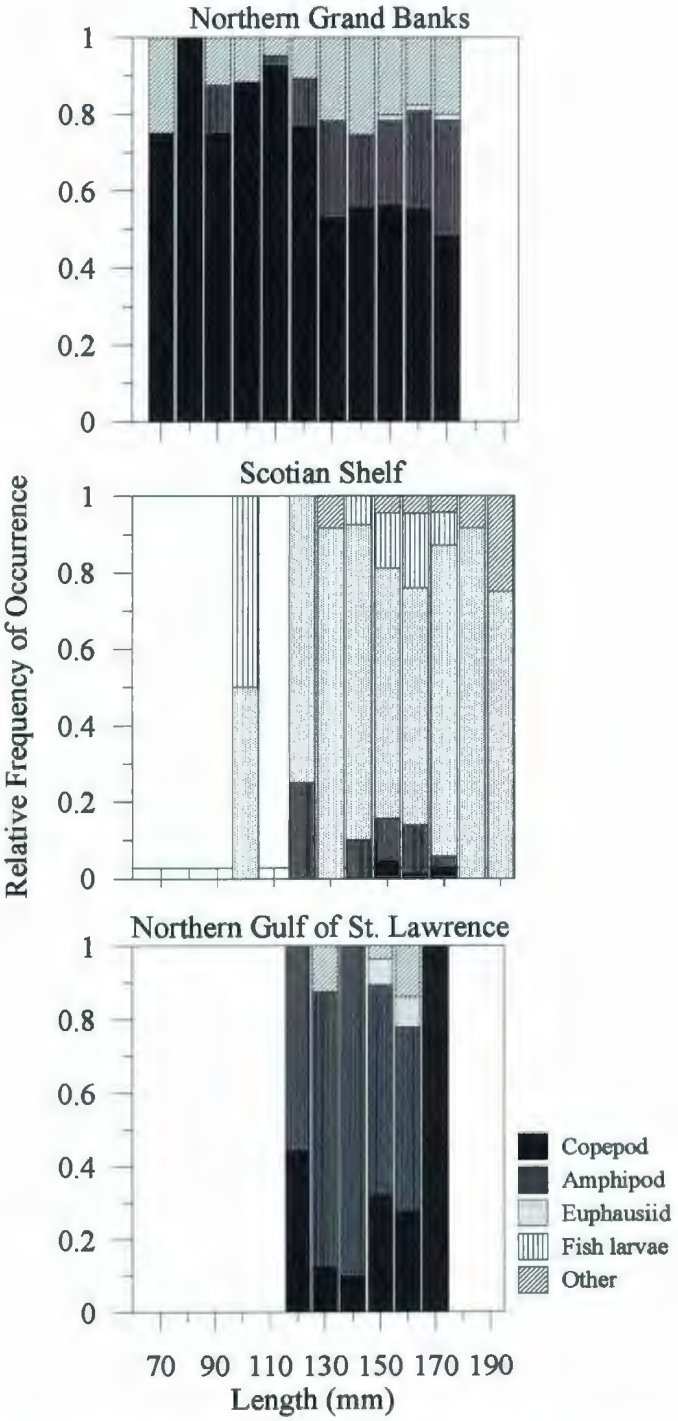

Figure 1.6 Relative frequency of occurrence of main prey categories across all capelin lengths (immature and maturing fish) for the northern Grand Banks, Scotian Shelf, and northern Gulf of St. Lawrence, in the spring of 2004.

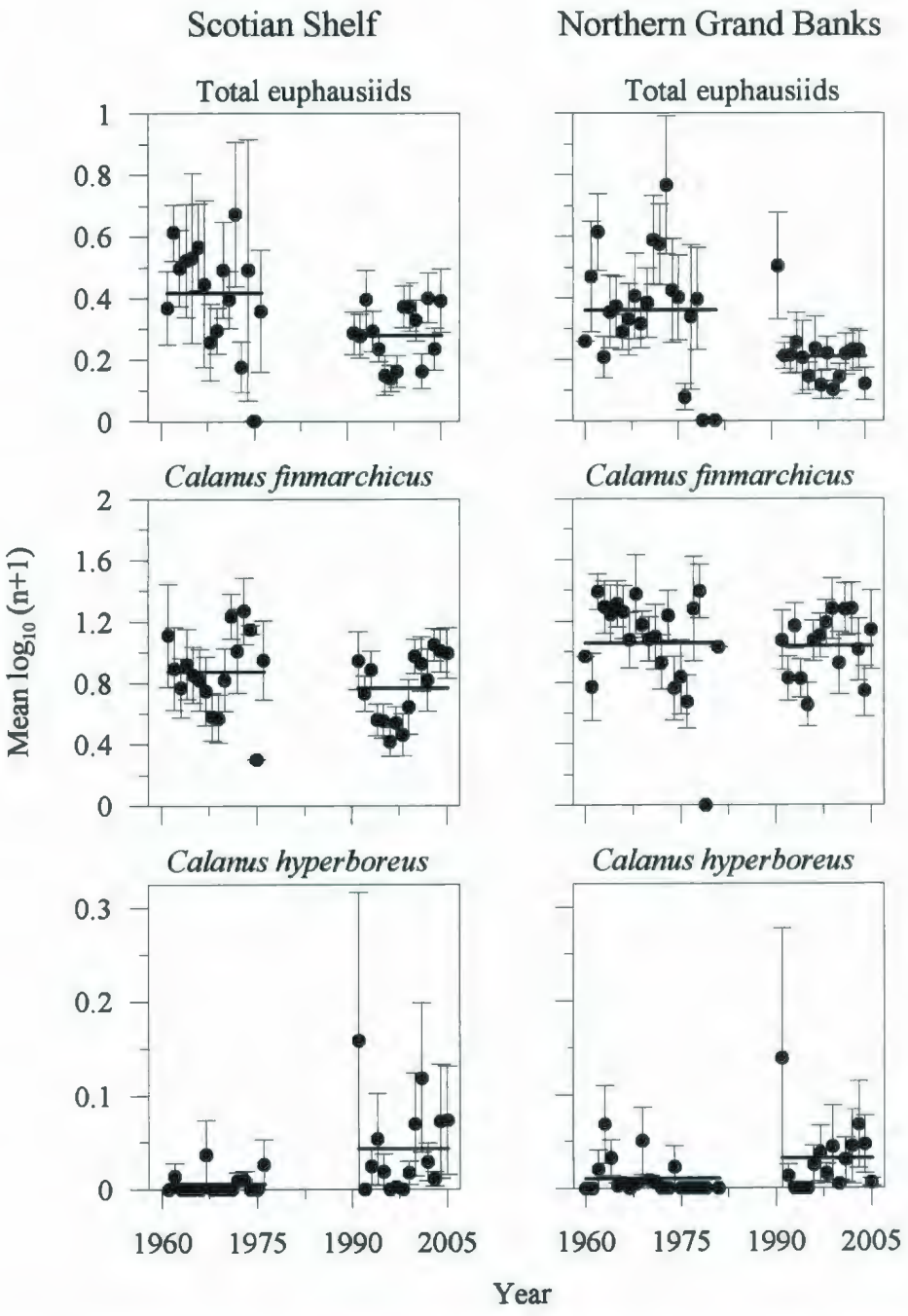

Figure 1.7 Yearly means and standard errors for log abundance of total euphausiids, *C. finmarchicus*, and *C. hyperboreus,* on the Scotian Shelf and northern Grand Banks. Overall means for the two time-periods are presented (northern Grand Banks 1960–1981 and 1991–2005, Scotian Shelf 1961–1976 and 1991–2005).

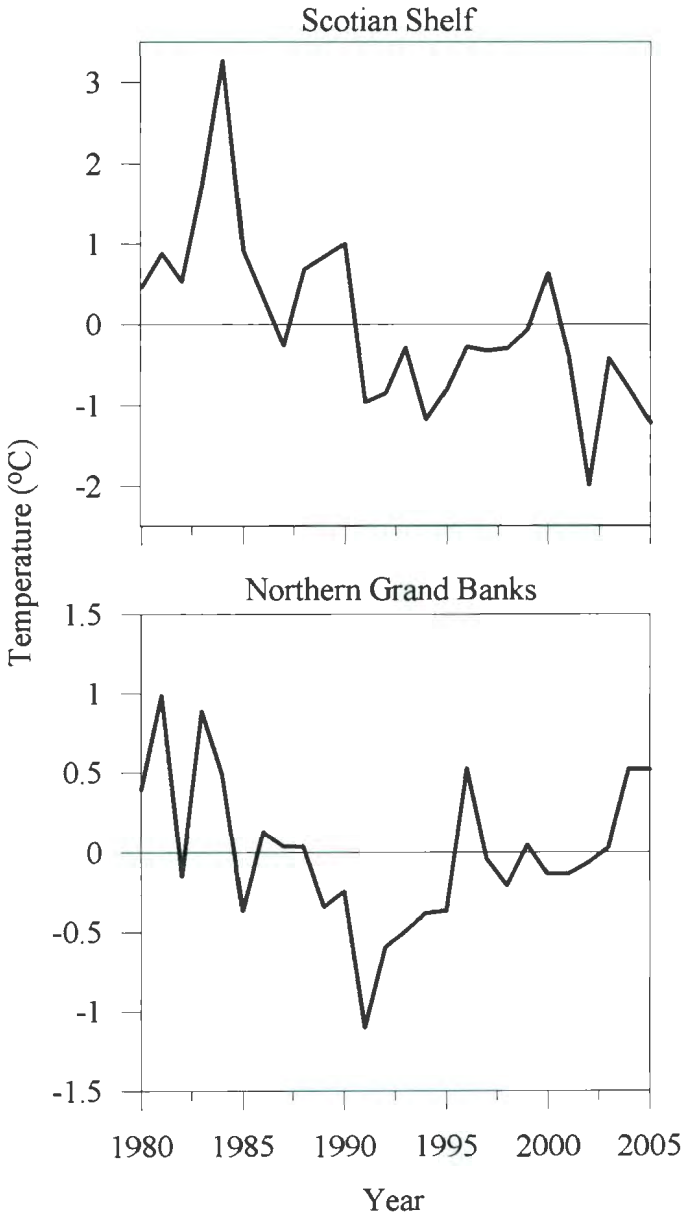

Figure 1.8 Vertically integrated temperature time series for the Louisbourg line, 0-240 m on the Scotian Shelf, and Station 27, 0-180 m on the northern Grand Banks, from 1980 to 2005.

CHAPTER 2. DID A TOP-DOWN CASCADE CREATE DIET COMPETITION BETWEEN GRAND BANKS CAPELIN (*MALLOTUS VILLOSUS*) AND NORTHERN SHRIMP (*PANDALUS BOREALIS*)?

2.1 Abstract

During the cold period of the late 1980s to early 1990s on the northern Grand Banks, the length, condition, and abundance of capelin (*Mallotus villosus*) declined in tandem with behavioural changes and a rapid decline in Atlantic cod (*Gadus morhua*), while northern shrimp (*Pandalus borealis*) increased in abundance. These biological changes have persisted with rising temperatures since 1996. A decline in cod predation has been suggested to have led to the increase in shrimp, but there is no evidence of an increase in capelin, the chief prey of cod. A possible explanation of this conundrum is a top-down cascade in which the increased shrimp out-competed capelin for planktonic food, leading to their decline. A comparison of stomach contents, however, indicated little dietary overlap, with capelin feeding mostly on zooplankton, especially copepods and amphipods, while shrimp fed mostly on polychaetes and perhaps detritus. Moreover, differences in stable isotope signatures and stomach contents agreed, indicating a more pelagic diet for capelin and a more benthic diet and lower trophic position for shrimp (trophic position values of 3.60 ± 0.03 for capelin and 3.12 ± 0.03 for shrimp). Capelin exhibited very high trophic fractionation for $\delta^{15}N$ (4.74‰), indicative of nutritional stress and poor condition. Overall, these data provide little support for the diet competition

hypothesis (between capelin and shrimp), as a result of a top-down cascade initiated by the decline of Atlantic cod.

2.2 Introduction

In the late 1980s to early 1990s, the Northwest Atlantic experienced below average temperatures (Drinkwater, 2002). The key forage fish species on the northern Grand Banks is the capelin (*Mallotus villosus*), a pelagic schooling zooplankton feeder (Gerasimova, 1990; O'Driscoll *et al.*, 2001). During the early 1990s, capelin exhibited major changes in distribution (Frank *et al.*, 1996), abundance (Carscadden and Nakashima, 1997), and vertical migratory behaviour (Mowbray, 2002), and spawning occurred later in the season (Carscadden *et al.*, 1997). In addition, body size and condition declined, and showed little recovery as temperatures increased during the mid to late 1990s (Carscadden and Frank, 2002; Carscadden *et al.* 2002; Colbourne *et al.*, 2005; Obradovich and Rose, submitted).

On the northern Grand Banks, *Pandalus borealis* (hereafter shrimp) increased rapidly in abundance during the late 1980s to early 1990s (Lilly *et al.*, 2000; DFO, 2006). Like capelin, shrimp feed on zooplankton (including euphausiids and calanoid copepods) in the North Sea (Wienberg, 1981), the fjords of Norway (Hopkins *et al.*, 1993), the Barents Sea (Berenboim, 1981) and Alaska (Barr, 1970), possibly during diel vertical migrations (Barr, 1970; Berenboim, 1981; Wienberg, 1981). In the Gulf of St. Lawrence, a mass balance inverse modelling study estimated that zooplankton comprised approximately 55% of the shrimp diet (Savenkoff *et al.*, 2006). Hence, the diet of capelin and shrimp on the northern Grand Banks might be expected to overlap. If so, the increase

in shrimp biomass during the 1990s could have reduced the availability of zooplankton, limiting capelin growth and condition and the potential for increases in these traits when marine temperatures increased in the mid-1990s. There have been no studies of potential competition between shrimp and pelagic fishes (Bergström, 2000). In freshwater systems, however, competition for prey between a pelagic fish and an invertebrate has been documented, which resulted in reduced fish size (Spencer *et al.*, 1991). I hypothesized that prey consumption by capelin and shrimp would overlap significantly, and suggest competition between these species, thus providing a mechanism to explain the persistence of reduced growth and condition in capelin in the warmer waters of the past decade.

Any interaction between Grand Banks shrimp and capelin has broader ecosystem implications. The increase in shrimp and decline in capelin occurred concurrently with the decline of their major predator, Atlantic cod (*Gadus morhua*) (Figure 2.1), which has been suggested as the cause of the shrimp increase, through a release from predation (Lilly *et al.*, 2000; Worm and Myers, 2003). In contrast, capelin, formerly the main prey of this cod stock, did not increase (Figure 2.1), suggesting that there is more to these interactions than simply removal of predation (e.g. Lilly *et al.*, 2000). Competition among cod prey could play a role. For example, if the cod decline released shrimp from predation, with the predator-free shrimp now out-competing capelin, a top-down cascade of trophic effects would be evident. On the other hand, a lack of competition for food would not support the trophic cascade and suggest another mechanism such as bottom-up forcing through the food web.

To assess dietary overlap, stomach contents and muscle isotope signatures can be compared. Stomach contents provide a short term view of diet, whereas isotope signature

turnover takes place over several months (Lorrain *et al.*, 2002) or longer (Hesslein *et al.*, 1993), and thus reflects a cumulative diet. The carbon signature of a consumer strongly reflects that of its prey, as the stable isotope ratio increases only 0.8‰ between prey and predator (DeNiro and Epstein, 1978; Vander Zanden and Rasmussen, 2001). In addition, in marine ecosystems, stable isotope ratios for carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) provide a measure of the benthic versus pelagic character of an organism's diet (France, 1995; Davenport and Bax, 2002; Sherwood and Rose, 2005). Stable nitrogen isotope ratios ($^{15}N/^{14}N$ or $\delta^{15}N$) are a measure of food chain length, hence of trophic position (TP) (Vander Zanden *et al.*, 1997), with the nitrogen stable isotope ratio increasing on average by 3.4‰ per trophic level (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001).

The objectives of this paper were to test the diet competition hypothesis by assessing stomach contents and stable isotope ratios (nitrogen and carbon) for a large size range of both capelin and shrimp from the northern Grand Banks, and to examine the broader ecosystem implications of the outcome.

2.3 Materials and Methods

Capelin and shrimp from the northern Grand Banks were sampled in the spring (mid to late May) of 2004 from the CCGS Teleost, employing either a Campelen 1800 bottom trawl or an IGYPT midwater trawl towed at depths of 20-310 m for 11-60 min (Figure 2.2). For both species, the widest available sizes were sampled. Up to 100 capelin per 1 cm size group were measured immediately after capture (n=499). For shrimp, up to 25 specimens were selected per survey area (inshore, at the shelf edge, in the north, and in

the south), then bagged and frozen at -20°C for subsequent measurement (total sampled n=128). All capelin and shrimp specimens were measured for length (± 1 mm for capelin, ± 0.01 mm for shrimp), body weight (± 0.1 g), gonad weight (± 0.1 g), and stomach weight (± 0.01 g), and gonads were examined to determine sex, and maturity. Maturing specimens were separated from immature ones by the presence of eggs/sperm, but were not considered mature if the gonads were still small and sexual products were not free-flowing. For capelin, total length was measured parallel to the lateral axis, from the tip of the snout to the upper lobe of the caudal tail; for shrimp, carapace length was measured parallel to the lateral axis, from the mid-orbit to the mid dorsal point. Stomachs were collected (foregut of shrimp) and preserved in 5% formalin made with sodium borate-buffered seawater. Up to four capelin per 1 cm size group were bagged and frozen (after measurement) at -20°C, for later stable isotope analysis. To obtain zooplankton samples, Bongo nets (63 cm in diameter, mesh size 505 μm) were towed vertically from 20 m to the surface. All Bongo tow samples were sorted at-sea into major taxa (e.g. Copepoda, Euphausiacea, and Amphipoda) and frozen in vials at -20°C. The large euphausiid, *Meganyctiphanes norvegica*, was collected from the trawl net and frozen in a vial at -20°C. Total length, from the front of the eye to the tip of the tail, along the lateral axis, was measured for all zooplankton except copepods, for which the lateral carapace length was measured.

Stomach contents, from the formalin-preserved stomachs, were washed and examined with a dissecting microscope. Prey items were sorted into categories based on major taxonomic level (class or order) and wet weight was obtained for each category. After analysis, all stomachs and prey items were preserved in 70% ethanol and saved for

future identification. Frequency of occurrence of prey items was calculated relative to the total number of stomachs sampled for a given size range of capelin or shrimp, and differences were tested with Chi-square analyses of contingency tables.

To measure stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in capelin, shrimp, and selected zooplankton species, tissue samples (~1-2 g) were collected, stored in 1.5 mL centrifuge vials, and frozen at -20°C: dorsal muscle tissue (anterior to the first dorsal fin) for capelin, caudal muscle tissue for shrimp, and whole body for zooplankton species. Isotope samples for the smaller zooplankton species (*Thysanoessa raschii*, *Parathemisto libellula*, small hyperiids, *Calanus hyperboreus*, *Calanus glacialis*, *Calanus finmarchicus*, and *Metridia longa*) contained multiple individuals of the same species in each vial to provide sufficient material for analysis, while samples of the larger zooplankton species (*M. norvegica* and *Thysanoessa inermis*) contained single individuals. Tissue/whole body samples were dried in a drying oven at 75°C for 48 hours, pulverized to a fine powder using a mortar and pestle, then analyzed at the G. G. Hatch Stable Isotope Laboratory at the University of Ottawa, Canada, for nitrogen and carbon isotope composition. Samples were packed in tin capsules and combusted to N_2 (to measure stable nitrogen isotopes) and CO_2 (to measure stable carbon isotopes) on a CE 1110 Elemental Analyser, followed by gas chromatograph separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope ratio mass spectrometer coupled with a ConFlo III. Stable isotope ratios are expressed in the delta (δ) notation with units of permil (parts per thousand, ‰). δ values represent the difference in the isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) from a standard (Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$)

and were calculated as $\delta^{H}X = [(R_{sample}/R_{standard}) - 1] * 1000$, where R is the ratio of the isotopes (Fry, 2006).

Stable isotope samples were simultaneously measured for percent carbon and percent nitrogen to provide a C/N ratio. C/N ratio is a proxy for lipid content, as lipids are nitrogen poor relative to other biochemical molecules (McConnaughey and McRoy, 1979; Rau *et al.*, 1992). $\delta^{13}C$ tends to decrease in animal tissues (including fish) as the lipid content increases (Tieszen *et al.*, 1983; Rau *et al.*, 1992). Therefore, I tested for differences in $\delta^{13}C$ with changes in the C/N ratio, in each species, by regression. Where significant, C/N ratio was incorporated as a covariate in further analyses of $\delta^{13}C$, for statistical control.

$\delta^{15}N$ signatures of invertebrates and fish on the northern Grand Banks vary geographically (Sherwood and Rose, 2005). I tested for a similar effect by dividing my samples geographically and using analysis of variance (ANOVA). Capelin samples were grouped into inshore (Trinity Bay) and offshore (elsewhere on the shelf) samples. No shrimp samples were available from Trinity Bay, hence shrimp samples were separated into three groupings: near-shore, shelf edge, and locations between those two groups (i.e. near-shore to the shelf edge). When significant differences were found, the geographic grouping variable was incorporated as a random factor in further analyses of $\delta^{15}N$, for statistical control. In addition, I tested for differences in $\delta^{13}C$ and $\delta^{15}N$ between species (by ANOVA or analysis of covariance (ANCOVA)) and with length (by multiple regression or ANCOVA).

To further examine the potential for trophic competition, I compared TP of shrimp and capelin, and calculated original trophic fractionation factors to measure changes in

the stable isotope ratios (carbon and nitrogen) between capelin and their prey. Original trophic fractionation values for $\delta^{13}C$ ($\Delta\delta^{13}C$) and $\delta^{15}N$ ($\Delta\delta^{15}N$) for capelin were calculated based on the diet proportions of prey items and their respective stable isotope signatures, following Sherwood and Rose (2005). For example, trophic fractionation for $\delta^{13}C$ was calculated as:

$$\Delta\delta^{13}C = \delta^{13}C_{capelin} - \left(\sum_{i=1}^{n} P_i * \delta^{13}C_i\right) \quad (1)$$

where $\delta^{13}C_{capelin}$ is the mean signature for all capelin in the population, $\delta^{13}C_i$ is the mean signature for the *i*th prey item in the diet of capelin in that population, and P_i is the proportion by weight of the *i*th prey in the capelin diet. P_i is calculated as:

$$P_i = \frac{W_i}{W_{total}} \quad (2)$$

where W_i is the total weight (g) of the *i*th prey item in all capelin stomachs of the population and W_{total} is the total weight (g) of all prey items in all capelin stomachs of that population. Trophic fractionation values were calculated based on all capelin sampled (n=499). TP for capelin and shrimp sampled offshore was calculated as:

$$TP = \frac{(\delta^{15}N_{con} - \delta^{15}N_{base})}{\Delta\delta^{15}N} + TL_{base} \quad (3)$$

where $\delta^{15}N_{con}$ is the stable nitrogen isotope signature of the consumer (capelin or shrimp), $\delta^{15}N_{base}$ is the stable nitrogen isotope signature of a baseline consumer from the same ecosystem, and TL_{base} is the estimated trophic level of the baseline consumer. A mix of zooplankton (copepods, amphipods, and euphausiids), sampled offshore, defined my baseline consumer and I assumed a TL of 2.2, based on trophic position estimates for

amphipods and euphausiids from Sherwood and Rose (2005), and the assumption that all small copepods are herbivorous (TL=2). Baseline consumers typically vary significantly in $\delta^{15}N$ with changes in $\delta^{13}C$ (Vander Zanden and Rasmussen, 1999; Sherwood and Rose, 2005), thus $\delta^{15}N_{base}$ was calculated as:

$$\delta^{15}N_{base} = m * (\delta^{13}C_{con} - \Delta\delta^{13}C) + b \quad (4)$$

where m and b are the slope and y-intercept, respectively, of the $\delta^{15}N$- $\delta^{13}C$ regression for all offshore baseline consumers, and $\delta^{13}C_{con}$ is the stable carbon isotope signature of the consumer. Global averages of 0.8‰ for $\Delta\delta^{13}C$ and 3.4‰ for $\Delta\delta^{15}N$ were used (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001), and not the initial trophic fractionation values. Differences in the TP of capelin and shrimp were tested by ANOVA. For all analyses, the criterion for significance (α) was set at 0.05 and residuals were examined to evaluate the assumptions for p values.

2.4 Results

Capelin and shrimp differed markedly in their spring prey consumption, as assessed by stomach contents (Table 2.1). Capelin, on average, were more frequent consumers of copepods (χ^2=142.842, df=1, p<0.001), amphipods (χ^2=19.019, df=1, p<0.001), and other prey (χ^2=8.081, df=1, p=0.004), while shrimp typically consumed more polychaetes (χ^2=24.193, df=1, p<0.001) (Table 2.1). Euphausiids were infrequently consumed by both species (χ^2=1.033, df=1, p=0.310), showing up only in the stomachs of the largest capelin sampled (Table 2.1). Capelin stomachs were more likely to be empty

than were the stomachs of shrimp (χ^2=8.883, df=1, p=0.003) (Table 2.1). More shrimp stomachs contained only unidentifiable materials (χ^2=185.835, df=1, p<0.001), although stomachs from juvenile capelin (70-80 mm) also frequently contained unidentifiable material (Table 2.1). When individuals with no identifiable stomach contents were removed from the analyses (Table 2.1), there was no difference in the average consumption of amphipods (χ^2=3.670, df=1, p=0.055), euphausiids (χ^2=0.432, df=1, p=0.511) or other prey (χ^2=0.285, df=1, p=0.593) between capelin and shrimp, but capelin were still more frequent consumers of copepods, on average (χ^2=59.682, df=1, p<0.001), while shrimp typically consumed polychaetes more frequently (χ^2=86.803, df=1, p<0.001). For this subset of the data, no difference in the frequency of empty stomachs (χ^2=0.075, df=1, p=0.784) between capelin and shrimp was detected.

Stable isotope signatures for capelin, shrimp, and zooplankton are presented in Table 2.2. As $\delta^{13}C$ signatures varied significantly with C/N ratio in shrimp ($F_{1,25}$=4.954, p=0.035, r^2=0.165), but not in capelin ($F_{1,32}$=1.237, p=0.274, r^2=0.037) and also differed significantly among species (ANOVA, $F_{4,89}$=92.204, p<0.001), C/N ratio was included as a covariate in all subsequent analyses of $\delta^{13}C$. In addition, $\delta^{15}N$ signatures varied significantly with geographic grouping for capelin (ANOVA, $F_{1,32}$=11.479, p=0.02) and shrimp (ANOVA, $F_{2,24}$=16.841, p<0.001). Thus, geographic grouping was included as a random factor in all subsequent analyses of $\delta^{15}N$ signatures.

$\delta^{13}C$ and $\delta^{15}N$ for capelin dorsal muscle tissue averaged 2.51‰ lower (ANCOVA, covariate C/N ratio, $F_{1,58}$=304.687, p<0.001) and 1.16‰ higher (ANOVA, random factor geographic grouping, $F_{1,55}$=35.657, p<0.001) respectively, than for shrimp caudal muscle tissue (Table 2.2, Figure 2.3). Values were not lipid-corrected because the C/N ratios of

capelin and shrimp muscle tissue were very similar (Table 2.2). $\delta^{13}C$ values differed significantly across Euphausiacea, Amphipoda, and Copepoda (ANCOVA, covariate C/N ratio, $F_{2,30}$=10.692, p<0.001). A *post hoc* Tukey test showed that the mean $\delta^{13}C$ signatures of amphipods and copepods differed from that of euphausiids (p=0.003 and p<0.001 respectively), but not from each other (p=0.438). Similarly, $\delta^{15}N$ signatures differed significantly among the zooplankton taxa (ANOVA, random factor geographic grouping, $F_{2,19}$=9.129, p=0.002). A *post hoc* Tukey test demonstrated that the mean $\delta^{15}N$ signatures of Amphipoda and Copepoda did not differ from each other (p=0.881), but both differed from Euphausiacea (p=0.002 for Amphipoda and p=0.017 for Copepoda). $\delta^{13}C$ values of the zooplankton were not corrected for lipid content because lipid-corrected prey values would alter the mixing models for trophic position calculation and trophic fractionation values. $\delta^{13}C$ signatures did not vary with length (covariate C/N ratio) for shrimp, *P. libellula*, or Copepoda, but increased with length for capelin (Table 2.3). $\delta^{15}N$ signatures did not vary significantly with body length (random factor geographic grouping) for capelin, shrimp, *P. libellula*, or Copepoda (Table 2.3).

Mean $\delta^{15}N$ signature for shrimp varied with longitude (ANOVA, $F_{4,22}$=13.686, p<0.001), with higher $\delta^{15}N$ signatures inshore (west) and lower $\delta^{15}N$ signatures at the shelf edge (east) (Figure 2.4). The amphipod, *P. libellula*, appeared to follow a similar trend in $\delta^{15}N$ signature relative to longitude, but the small sample size prevented further analysis. $\delta^{13}C$ signatures did not vary with geographic grouping for capelin (ANCOVA, covariate C/N ratio, $F_{1,31}$=0.031, p<0.861) or shrimp (ANCOVA, covariate C/N ratio, $F_{2,23}$=1.845, p<0.181).

Original trophic fractionation factors for both $\delta^{13}C$ and $\delta^{15}N$, based on the proportions of the major prey items in their spring diet, were calculated for capelin using Eq. (1) and Eq. (2) (Table 2.4). For capelin of all sizes, trophic fractionation estimates averaged -0.12‰ for $\delta^{13}C$, and 4.74‰ for $\delta^{15}N$ (Table 2.4).

TP was calculated for capelin and shrimp using Eq. (3) and (4). $\delta^{15}N$ did not differ with changes in $\delta^{13}C$ for offshore zooplankton ($F_{1,22}$=0.165, p=0.698, r^2=0.007), but slope and y-intercept parameters from the regression equation ($\delta^{15}N = 0.151 * (\delta^{13}C) + 10.799$) were used in Eq. (4) to calculate $\delta^{15}N_{base}$. TP (mean ± 1 SE) differed between capelin (3.60 ± 0.03) and shrimp (3.12 ± 0.06) (ANOVA, $F_{1,53}$=63.310, p<0.001). TP did not vary with length for capelin ($F_{1,29}$=0.013, p=0.911, r^2<0.001) or shrimp ($F_{1,22}$=0.021, p=0.886, r^2=0.001). Correcting for lipids (method from McConnaughey and McRoy, 1979) prior to calculating TP increased the TP only marginally, by 0.03 for capelin and 0.05 for shrimp.

2.5 Discussion

Diets of capelin and shrimp on the northern Grand Banks in spring 2004 differed greatly, and the two species had very different stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$). Together, these findings provide evidence to reject the null hypothesis of no difference between diets of these species. Capelin stomachs contained mainly copepods and amphipods, which is consistent with historical information on diet on the northern Grand Banks, except that euphausiids used to appear frequently (Gerasimova, 1994; O'Driscoll *et al.*, 2001). In contrast, the main items in the shrimp guts were polychaetes and amphipods. Earlier studies on shrimp diet have suggested that both pelagic zooplankton

(including calanoid copepods, amphipods, and euphausiids) and macrobenthic prey (such as polychaetes) form an important part of the diet (Barr, 1970; Berenboim, 1981; Wienberg, 1981; Hopkins *et al.*, 1993; Savenkoff *et al.*, 2006). A large proportion of shrimp stomachs contained only unidentifiable material, which may have been detritus or digested material from prey items. Detritus may contribute to lipid formation in shrimp, but the fatty acids associated with bottom sediment feeding are not common in shrimp tissue (Hopkins *et al.*, 1993). Savenkoff *et al.* estimated that detritus forms over 25% (by weight) of the shrimp diet, but Wienberg (1981) dismissed detritus as nutritionally unimportant to shrimp. Some studies do not report consumption of detritus (Barr, 1970; Berenboim, 1981). In the present study, considering only individuals with some identifiable stomach contents increased the apparent importance of polychaetes and copepods in the diet of shrimp.

The mean $\delta^{13}C$ signature for shrimp was enriched by 2.51‰ relative to the mean signature for capelin, consistent with the values of Sherwood and Rose (2005). These results indicate a more benthic diet for shrimp and a more pelagic diet for capelin (France, 1995; Davenport and Bax, 2002). The $\delta^{13}C$ signature measured for capelin was comparable with the $\delta^{13}C$ values for copepods and amphipods and with the higher frequency of these items in the capelin diet. A benthic $\delta^{13}C$ signature for shrimp is consistent with the present stomach contents and the polychaete $\delta^{13}C$ signature reported by Sherwood and Rose (2005). It may also reflect shrimp consumption of detritus, which is enriched in ^{13}C relative to phytoplankton (McConnaughey and McRoy, 1979). While shrimp diets rich in euphausiids have been reported in the Barents and North Seas (Berenboim, 1981; Wienberg, 1981; Hopkins *et al.*, 1993), there is no evidence in the

present study of euphausiid consumption by shrimp on the northern Grand Banks, although their $\delta^{13}C$ signatures are similar (Figure 2.3). It is noteworthy that euphausiids have declined on the northern Grand Banks since the early 1990s (Sameoto, 2004). Thereafter, euphausiids (particularly *T. raschii*) declined in the diet of mature capelin (O'Driscoll *et al.*, 2001; Mowbray, 2002; Obradovich and Rose, submitted), coincident with the increase in shrimp abundance. Although reports of fish-invertebrate interactions in marine environments are few, diet shifting or competition-based food niche contraction has been shown repeatedly in freshwater lakes (e.g. Persson and Hansson, 1999; Vander Zanden *et al.*, 1999), sometimes as a consequence of one competitor being more abundant (Persson, 1983).

Among the small zooplankton taxa, $\delta^{13}C$ signatures reflected size differences among species. The larger zooplankters, *P. libellula* and *C. hyperboreus*, displayed slightly enriched $\delta^{13}C$ signatures compared to smaller zooplankters (small hyperiids, *C. glacialis*, *C. finmarchicus*, and *M. longa*). As $\delta^{13}C$ typically enriches by 0.8‰ between predator and prey (DeNiro and Epstein, 1978; Vander Zanden and Rasmussen, 2001), this difference is likely a result of their respective food chain length, rather than a measure of pelagic or benthic carbon sources. For the euphausiids, the *Thysanoessa* species were more benthic feeders than the large *M. norvegica*, and $\delta^{15}N$ values for the euphausiids were higher than other zooplankton, reflecting a more carnivorous diet (Berkes, 1976). In the present study, small zooplankton showed the greatest variation in $\delta^{15}N$ and $\delta^{13}C$, which reflects the high variability in the $\delta^{15}N$ and $\delta^{13}C$ of their nutrient sources and the rapid turnover of $\delta^{15}N$ in small invertebrates (e.g. Fry and Arnold, 1982).

Capelin and shrimp differed in their $\delta^{15}N$ signatures (corrected for their inshore-offshore position) with $\delta^{15}N$ enriched by 1.16‰ in capelin compared to shrimp, consistent with Sherwood and Rose (2005). $\delta^{15}N$ is a measure of food chain length or trophic position (Cabana and Rasmussen, 1994), but conversion of $\delta^{15}N$ to trophic position requires accounting for fractionation (the change in isotope ratios between prey and predator) and for differences in $\delta^{13}C$ signatures (Vander Zanden and Rasmussen, 1999). The present value for trophic fractionation of $\delta^{13}C$ for capelin ($\Delta\delta^{13}C$= -0.12‰) is lower than the global average, but within the range reviewed by Vander Zanden and Rasmussen (2001). A low value of $\Delta\delta^{13}C$ indicates that neither carbon isotope is preferentially assimilated during tissue formation and that the consumer $\delta^{13}C$ signature closely resembles that of its prey, in this case, copepods and amphipods. In contrast, the original trophic fractionation value for $\delta^{15}N$ ($\Delta\delta^{15}N$) for capelin in this study was 4.74‰, which exceeds the global average of 3.4‰ (Vander Zanden and Rasmussen, 2001). An elevated $\Delta\delta^{15}N$ may reflect a poor nutritional state in capelin, as nutritional stress and fasting can lead to catabolism of body proteins and an elevation in tissue $\delta^{15}N$ (Hobson *et al.*, 1993; Sherwood and Rose, 2005). Capelin condition has been poor on the northern Grand Banks since the early 1990s compared to other areas of the Northwest Atlantic (Carscadden and Frank, 2002; Obradovich and Rose submitted). Poor condition coincided with reduced spring euphausiid consumption (O'Driscoll *et al.*, 2001; Obradovich and Rose submitted) as compared to historical feeding (Gerasimova, 1994). Of note, $\delta^{15}N$ signatures of capelin did not change with length, indicating the lack of an ontogenetic diet shift from copepods to euphausiids, historically evident in capelin on the northern Grand Banks (Gerasimova, 1994).

Mean trophic position for capelin (3.60 ± 0.03) was greater than that of shrimp (3.12 ± 0.03). These values are higher than, but consistent in order with, previous offshore estimates for capelin (TP=3.32) and shrimp (TP=2.20) in this area (G. D. Sherwood, pers. comm.). In addition, other literature values for capelin (TP=3.6 from Lesage *et al.*, 2001) and pandalid shrimp (TP=3.0 from Fry, 1988) are very close to the present values. Diet studies show shrimp feed on herbivores and omnivores with some detrital consumption, raising their TP above herbivores (theoretical TP=2). Differences in TP can result from the mix of baseline consumers used to calculate TP. Sherwood and Rose (2005) may have underestimated TP of shrimp because they included that species in their group of baseline consumers. Error in the present TP calculations could result from the estimated TL_{base} of 2.2 for zooplankton, which assumes that small copepods are completely herbivorous, which may be violated for *M. longa* (Conover and Huntley, 1991), and that amphipods and euphausiids have a trophic level of 2.3 (Sherwood and Rose, 2005).

In conclusion, based on the analysis of diet and stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) of muscle tissue for capelin and shrimp on the northern Grand Banks, there is little evidence of an overlap in prey consumption that could indicate a potential for competition. Thus, the large increase in the abundance and distribution of pandalid shrimps during the 1990s (Lilly *et al.*, 2000; DFO, 2006) likely did not contribute to the observed changes in capelin size and condition that occurred during the same time period (e.g. Carscadden *et al.*, 1997; Carscadden and Frank; 2002; Carscadden *et al.*, 2002). The major and reciprocal changes in the abundance of these two major species in the Northwest Atlantic suggest that a common environmental cause could underlie changes in

abundance of both species. Finally, changes in capelin and shrimp abundance are unlikely to be solely attributed to the decline of their common major predator, Atlantic cod (i.e. a top-down cascade), as it appears that capelin have been under bottom-up control, independent of changes in shrimp biomass.

Table 2.1 Relative frequency of occurrence (%) of prey in capelin (10 mm length bins) and shrimp (2 mm length bins) stomachs, where n is the total number of stomachs sampled. Data in brackets are the relative frequency of occurrence (%) when stomachs containing only unidentifiable contents (column: Unid.) are excluded (n=457 for capelin and n=49 for shrimp).

Size		Relative frequency of occurrence (%)						
(mm)	n	Copepoda	Amphipoda	Euphausiacea	Polychaeta	Other	Unid [a]	Empty
Capelin								
70	45	13.3 (25.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.4 (8.3)	46.7	35.6 (66.7)
80	7	28.6 (40.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	28.6	42.9 (60.0)
90	14	42.9 (46.2)	7.1 (7.7)	0.0 (0.0)	0.0 (0.0)	7.1 (7.7)	7.1	35.7 (38.5)
100	43	69.8 (73.2)	0.0 (0.0)	0.0 (0.0)	4.7 (4.9)	4.7 (4.9)	4.7	20.9 (22.0)
110	57	66.7 (70.4)	1.8 (1.9)	0.0 (0.0)	1.8 (1.9)	1.8 (1.9)	5.3	26.3 (27.8)
120	55	78.2 (82.7)	12.7 (13.5)	0.0 (0.0)	1.8 (1.9)	7.3 (7.7)	5.5	12.7 (13.5)
130	51	66.7 (70.8)	31.4 (33.3)	0.0 (0.0)	3.9 (4.2)	23.5 (25.0)	5.9	23.5 (25.0)
140	50	66.0 (67.3)	22.0 (22.4)	0.0 (0.0)	6.0 (6.1)	24.0 (24.5)	2.0	24.0 (24.5)
150	52	69.2 (73.5)	26.9 (28.6)	1.9 (2.0)	5.8 (6.1)	21.2 (22.4)	5.8	21.2 (22.4)
160	87	79.3 (79.3)	36.8 (36.8)	2.3 (2.3)	4.6 (4.6)	20.7 (20.7)	0.0	11.5 (11.5)
170	38	76.3 (82.9)	47.4 (51.4)	2.6 (2.9)	18.4 (20.0)	15.8 (17.1)	7.9	10.5 (11.4)
Mean	499	59.7 (64.7)	16.9 (17.8)	0.6 (0.0)	4.3 (4.5)	11.9 (12.7)	10.8	24.1 (29.4)
Shrimp								
13	7	14.3 (33.3)	0.0 (0.0)	0.0 (0.0)	14.3 (33.3)	0.0 (0.0)	57.1	14.3 (33.3)
15	25	0.0 (0.0)	4.0 (12.5)	0.0 (0.0)	16.0 (50.0)	0.0 (0.0)	68.0	16.0 (50.0)
17	14	7.1 (20.0)	7.1 (20.0)	0.0 (0.0)	7.1 (20.0)	7.1 (20.0)	64.3	14.3 (40.0)
19	37	2.7 (8.3)	0.0 (0.0)	0.0 (0.0)	18.9 (58.3)	5.4 (16.7)	67.6	2.7 (8.3)
21	28	10.7 (27.3)	3.6 (9.1)	0.0 (0.0)	21.4 (54.5)	0.0 (0.0)	60.7	7.1 (18.2)
23	15	13.3 (25.0)	6.7 (12.5)	0.0 (0.0)	20.0 (37.5)	13.3 (25.0)	46.7	13.3 (25.0)
25	2	0.0 (0.0)	50.0 (50.0)	0.0 (0.0)	0.0 (0.0)	50.0 (50.0)	0.0	0.0 (0.0)
Mean	128	6.9 (16.2)	10.2 (14.9)	0.0 (0.0)	14.0 (36.2)	10.8 (16.0)	52.1	9.7 (25.0)

[a] Relative frequency of occurrence (%) of only unidentified material in the stomach. If a stomach contains prey items and unidentified material it is not included in this category.

Table 2.2 Stable isotope signatures, carbon to nitrogen ratios and length ranges for zooplankton (Euphausiacea, Amphipoda, and Copepoda), capelin, and shrimp.

		Length (mm)		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		C/N ratio	
Species/taxon	n	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Capelin	34	123.38	5.70	-20.61	0.07	12.43	0.10	3.52	0.02
Shrimp	27	19.31	0.57	-18.1	0.07	11.27	0.21	3.29	0.02
Euphausiacea									
M. norvegica	3	37.05	1.28	-20.09	0.10	9.22	0.12	5.01	0.23
T. raschii	3	13.89	1.10	-18.02	0.15	9.14	0.20	4.47	0.09
T. inermis	1	26.16		-18.46		9.76		4.41	
Mean				-18.97		9.26		4.69	
Amphipoda									
P. libellula	12	12.30	1.45	-20.14	0.19	7.74	0.24	5.91	0.24
Hyperiids	2	3.69	0.60	-20.75	0.25	6.98	1.39	5.92	0.17
Mean				-20.22		7.63		5.92	
Copepoda									
C. hyperboreus	3	5.28	0.10	-19.78	0.16	7.40	0.43	7.89	0.37
C. glacialis	3	3.80	0.14	-20.91	0.21	7.81	0.04	6.48	0.66
C. finmarchicus	3	2.55	0.09	-21.04	0.46	6.63	1.40	4.87	0.14
M. longa	3	2.59	0.08	-20.64	0.03	7.73	0.04	5.19	0.14
Mean				-20.59		7.40		6.10	

Table 2.3 Results of analyses of length effect on $\delta^{13}C$ signatures (multiple regression with C/N ratio as a covariate) and on $\delta^{15}N$ signatures (ANCOVA with geographic grouping as a random factor). Separate analyses were conducted for capelin, shrimp, *Parathemisto libellula*, and Copepoda.

	$\delta^{13}C$			$\delta^{15}N$			
Species/taxon	*F*	p	df [a]	*F*	p	df [a]	n
Capelin	7.044	0.003	2,31	0.031	0.862	1,31	34
Shrimp	2.406	0.112	2,24	0.292	0.594	1,23	27
P. libellula	2.915	0.106	2,9	1.466	0.28	1,5	12 (9)[b]
Copepoda	3.321	0.083	2,9	2.488	0.213	1,3	12 (6)[b]

[a] Degrees of freedom are listed as numerator, denominator.

[b] The number in brackets represents n for the ANCOVAs for *P. libellula* and Copepoda. A reduced number of data points were included in the analysis due to the inability to designate some samples as near-shore, shelf, or shelf edge.

Table 2.4 Trophic fractionation values ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) for northern Grand Banks capelin. Diet proportions (P_i), by weight, are based on stomach contents from all spring capelin collected (n=499) and represent the most common items. $\delta^{15}N$ and $\delta^{13}C$ signatures are based on values in Table 2.2.

	Pi (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Taxon			
Euphausiacea	0.02	-18.97	9.26
Amphipoda	0.26	-20.22	7.63
Copepoda	0.65	-20.59	7.40
Polychaeta	0.01	-18.00 [a]	16.60 [a]
Other zooplankton	0.06	-21.30 [b]	9.75 [b]
Overall diet signature		-20.49	7.68
Capelin signature		-20.61	12.43
Trophic fractionation		-0.12	4.74

[a] Value is from Sherwood and Rose (2005).

[b] Value is a composite of signatures for Cirripedia, mysids, and isopods from Sherwood and Rose (2005) and gelatinous zooplankton from Pepin and Dower (2007).

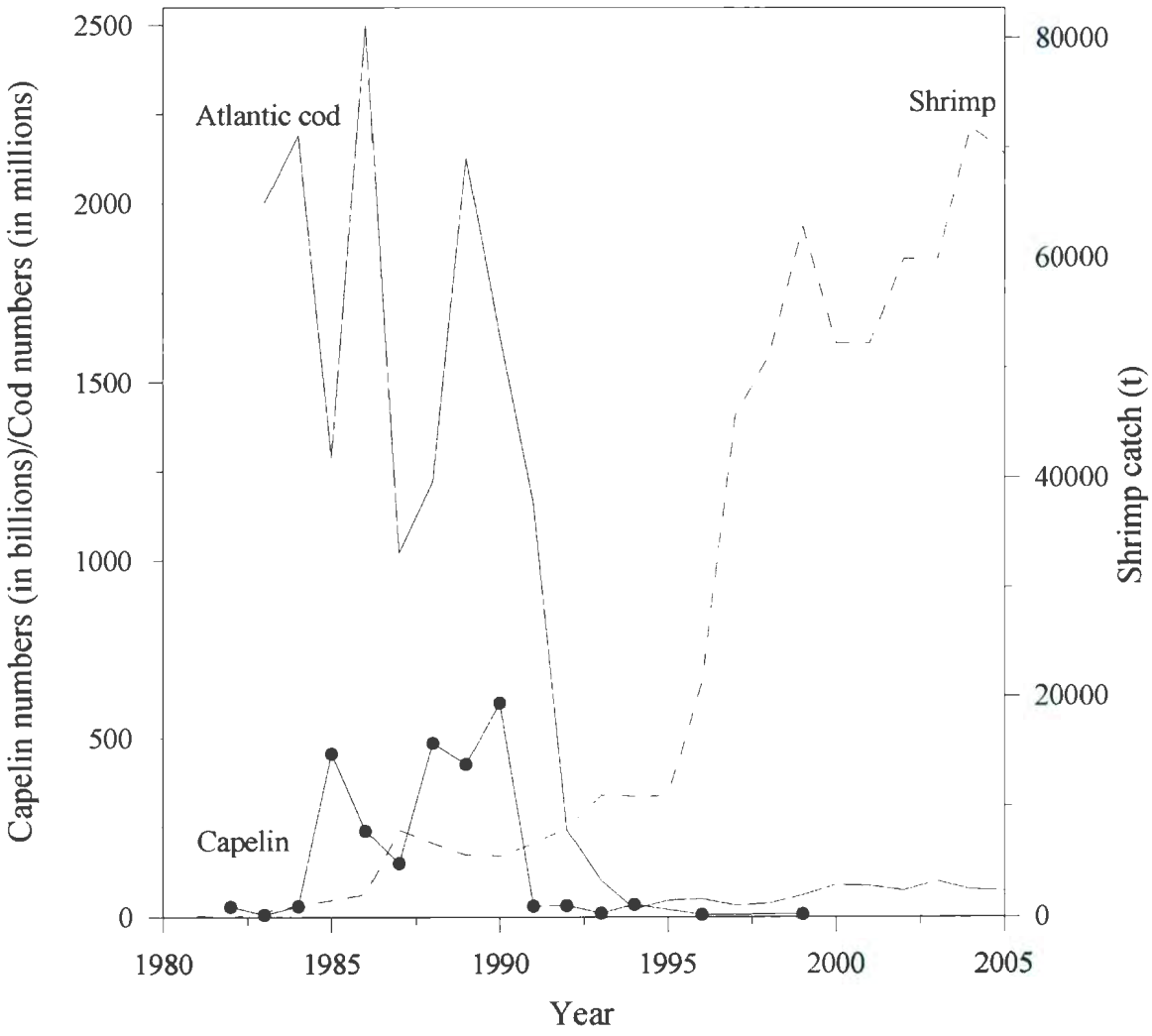

Figure 2.1 Abundance of capelin (in billions) from spring and autumn acoustic surveys of the northern Grand Banks (data from Miller, 1995; Miller, 1997; Mowbray, 2001), Atlantic cod (in millions) from autumn bottom-trawl surveys of the northern Grand Banks and southern Labrador (data from Lilly *et al.*, 2006), and shrimp catches from the northern Grand Banks and southern Labrador (data from Lilly *et al.*, 2000; DFO, 2006).

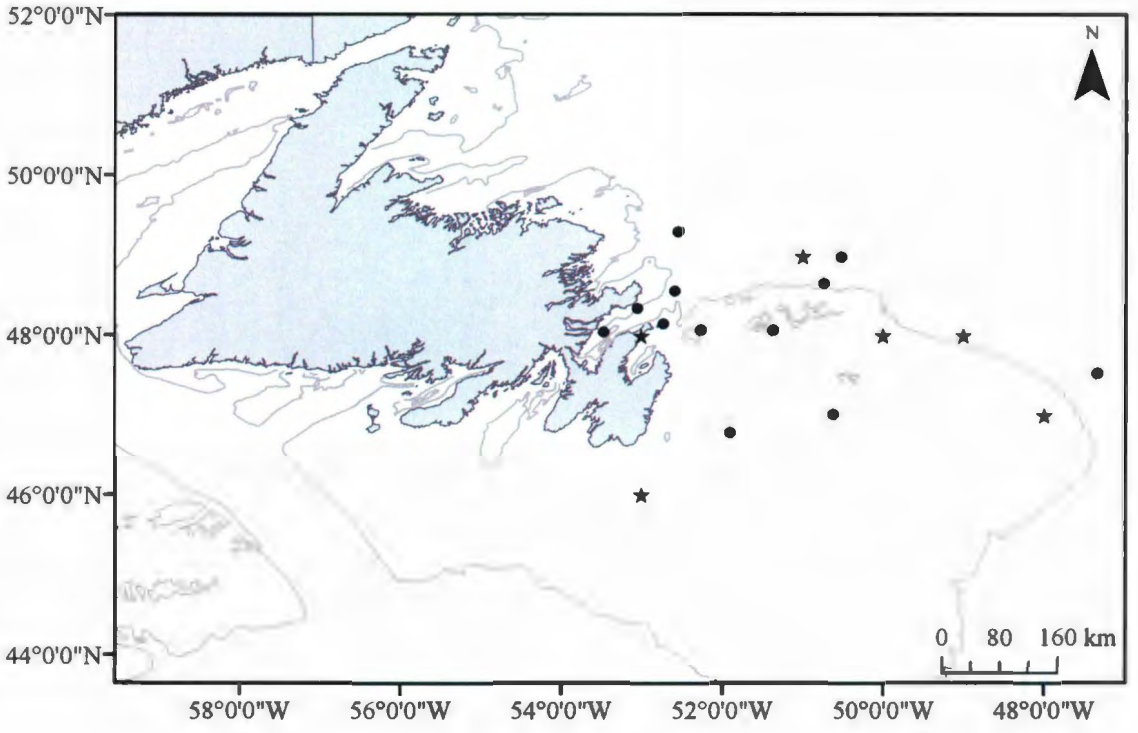

Figure 2.2 Sampling locations for capelin and shrimp on the northern Grand Banks, in spring 2004. Stars denote the location of sampling with concurrent Bongo tows.

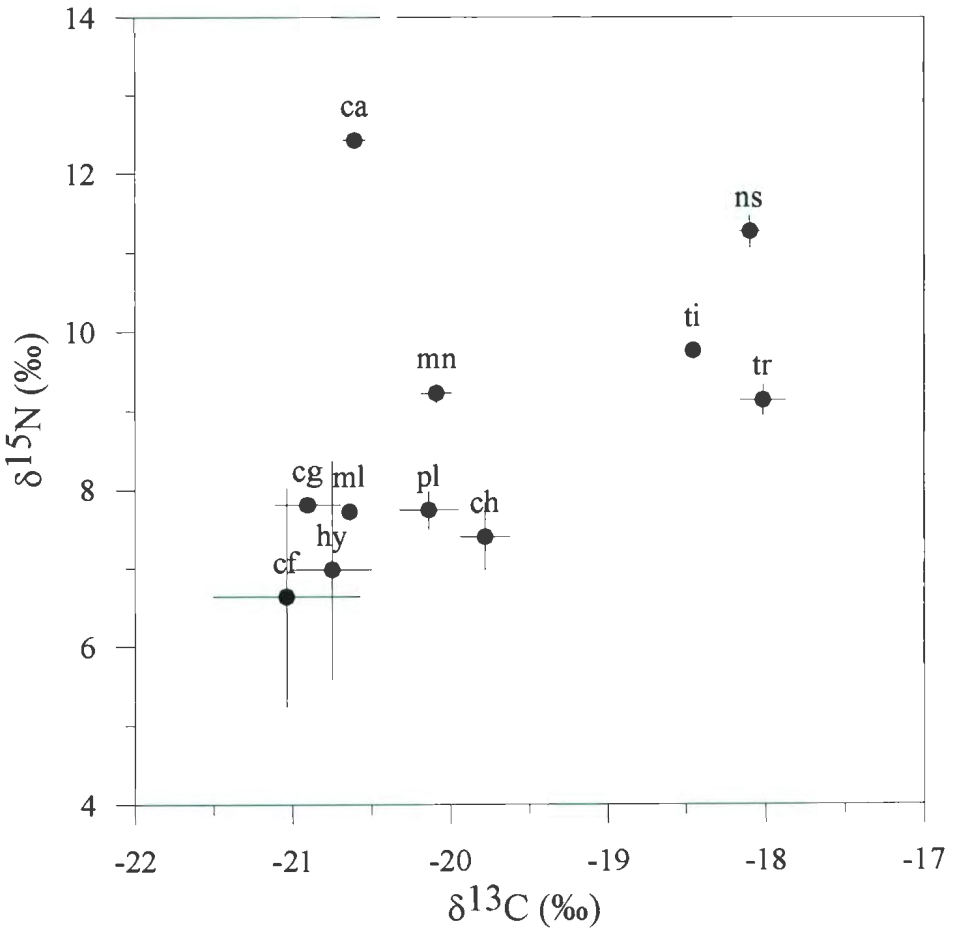

Figure 2.3 Mean values of $\delta^{15}N$ (± 1 SE) and $\delta^{13}C$ (± 1 SE) for capelin (ca), shrimp (ns), the euphausiids, *Meganyctiphanes norvegica* (mn), *Thysanoessa raschii* (tr), and *Thysanoessa inermis* (ti), the large hyperiid, *Parathemisto libellula* (pl), small hyperiids (hy), and the copepods, *Calanus hyperboreus* (ch), *Calanus glacialis* (cg), *Calanus finmarchicus* (cf), and *Metridia longa* (ml).

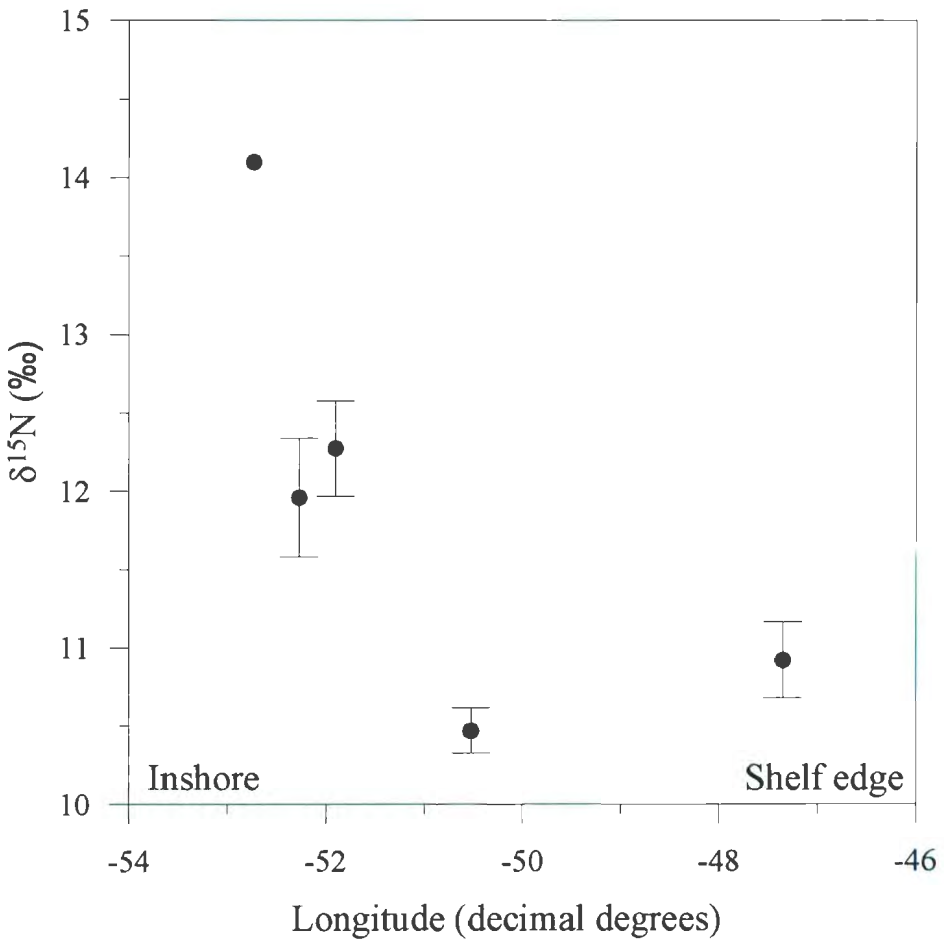

Figure 2.4 Mean value (± 1 SE) of $\delta^{15}N$ for shrimp collected along a longitudinal gradient, from west to east, on the northern Grand Banks.

SUMMARY

In this thesis, I examined the hypothesis that the persistence of changes in the biology of capelin (i.e. decreased mean mature length, condition, and abundance) on the northern Grand Banks, following the cold period of the early 1990s, resulted from a dietary deficiency. A comparative analysis of the condition, length-at-age, and diets of capelin from the northeast Newfoundland Shelf and northern Grand Banks (NGB), northeastern Scotian Shelf (SS) and northern Gulf of St. Lawrence (NSL) in the spring of 2004, showed that maturing SS capelin grew faster and attained superior length and condition than NGB capelin (NSL capelin were intermediate but sample size was too low for statistical comparison). SS capelin fed heavily on euphausiids in contrast to NGB capelin that fed mostly on copepods. NSL capelin fed on a mix of prey types, especially amphipods. Temperature did not provide a consistent explanation of these differences. A historical comparison of spring diets of Newfoundland capelin showed a steady decline in euphausiid consumption from the late 1980s onward, which was consistent with available Continuous Plankton Recorder data. Overall, my data suggested that bottom-up forcing of ecosystem change in the Northwest Atlantic has occurred, indexed by changing states of key zooplankters and capelin.

During the years of the changes in capelin biology, cod declined and shrimp increased in abundance on the Newfoundland and Labrador Shelf. Uncertainty remained as to if and how these factors could be related. The decline in cod could have released shrimp from predation (Worm and Myers, 2003), or favourable oceanographic changes may have increased their abundance (Parsons and Colbourne, 2000). If predation, then

why would capelin, cod's chief prey, not have increased too? I hypothesized that a top-down cascade could have occurred in which increased shrimp out-competed capelin.

The hypothesis that the prey consumption of these two species overlapped significantly creating competition for prey resources was tested. A comparison of feeding through investigation of stomach contents revealed that capelin more frequently consumed copepods, while shrimp more frequently consumed polychaetes. Stable isotope signatures indicated different carbon and nitrogen sources for these species, with capelin signatures suggesting a diet rich in copepods and amphipods, while shrimp signatures matched well with the signatures of euphausiids from the study, and those of polychaetes from other studies. Trophic fractionation factors (i.e. how isotope ratios change between the prey and the consumer) indicated that capelin on the northern Grand Banks may be in a state of nutritional stress, and relying upon the catabolism of their body proteins as a nitrogen source (Hobson *et al.*, 1993), which matches well with their observed poor condition. Trophic position of capelin was still higher than that of shrimp, indicating different roles as carnivores. Based on the analysis of diet and stable isotope signatures, there was no evidence of a significant overlap in prey consumption for capelin and shrimp on the northern Grand Banks. Thus, the large increase in the abundance and distribution of pandalid shrimps during the 1990s likely did not contribute to the observed changes in capelin biology that occurred during the same time period. The major and reciprocal changes in the abundance of these two major species in the Northwest Atlantic suggests that a common environmental cause could underlie changes in both species, but these changes in their abundance cannot be solely attributed to the decline of their common major predator, Atlantic cod (i.e. a top-down cascade).

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